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EVIDENCES OF RACIAL INFLUENCE IN A 25-YEAR TEST OF PONDEROSA PINE[1]

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INTRODUCTION

The need for discrimination in collecting and importing forest-tree seed for planting was effectively pointed out by European foresters about 50 years ago, and some experimental plantings of seed from different sources were made in Europe at that time. About the opening of the present century, Cieslar (*8*)[2] and Engler (*12*) began intensive systematic investigations of the influence of seed origin on forest trees. The results showed definitely that when seed from the northern part or the higher altitudes of a tree's natural range in Europe was planted in the southern part or at the lower altitudes, the resulting trees grew less rapidly and developed less well than trees grown in the same localities from seed of local origin; and that if the offspring of parents adapted to the long growing seasons of low latitudes and low altitudes were planted in a more severe climate, they failed to survive or were badly deformed by frost injury.

To test the suitability of Scotch pine seed from various sources for planting in given parts of Europe, it was agreed at the 1906 meeting of the International Union of Forest Experiment Stations that the various countries within the range of the species should undertake an intensive cooperative experiment. Seed was collected from 12 widely scattered sources and planted in 1907 and 1908 in typical localities in Germany, Belgium, Netherlands, Sweden, Hungary, Austria, and Russia. In 1908 and 1909 a similar experiment with Scotch pine was started in Switzerland. Summarizations of the 20-year results of the international experiment and the Swiss experiment, by Wiedemann (*35*) and Burger (*5*), respectively, confirmed the conclusions derived from the earlier studies and added greatly to knowledge of the subject. They also indicated definite localities the seed of which is suitable for planting in other stated localities in Europe. These experiments and others having to do with the significance of seed origin have given rise to a wealth of literature, the extent of which is indicated by a bibliography compiled by Champion (*7*) containing 166 titles.

In American forestry literature, attention was called to the importance of seed origin by Zon (*36*) in 1913 and by Toumey (*32*) in 1914. Since then Pearson (*24*), Eckbo (*11*), Roeser (*27*), Bates (*4*), Austin (*1*), Baldwin (*3*), and other American foresters have published discussions of the subject. It has been common practice in

[1] Submitted for publication July 20, 1939.

[2] Italic numbers in parentheses refer to Literature Cited, p. 886.

the United States to collect forest-tree seed wherever it happened to be abundant and easy to obtain, with little regard to suitability for the locality where trees were to be grown or to the growth characteristics, form, or resistance to frost and disease that the trees might inherit. Only recently has some slight attention been given to the subject by planting and seed-collecting agencies.

As early as 1911 Zon, then in charge of silvicultural research in the Forest Service, started progeny experiments patterned after those in Europe at several of the newly established forest experiment stations in the Western States. Of these experiments, in which several species were used, only a few with ponderosa pine (*Pinus ponderosa*) and one with Douglas fir (*Pseudotsuga taxifolia*) (*17*, *22*) are still in progress and are now yielding results.

The experiment with ponderosa pine discussed in this paper [3] is one of these early projects and is, therefore, practically contemporaneous with the afore-mentioned European experiments. Seedlings grown from seed collected in many widely separated localities within the natural range of ponderosa pine were planted on an area in northern Idaho. The first plantings were made in the fall of 1911. The observations reported here extended to 1935.

The purposes of the study were stated at the time of its initiation as follows: (1) To determine the suitability of ponderosa pine seed from different sources for planting in northern Idaho; (2) to ascertain heritable characteristics of growth, form, and hardiness, developed through adjustment of parents to local climates; and (3) to determine what limitations should be placed on the interchange of seed between localities of different climate.

Nothing was known of the pollinating parents as distinct from the cone-bearing parents, and no information was recorded as to individual characteristics of the latter. In practical artificial reforestation, however, in which seed must be collected on a large scale and the forester is not yet able to control or identify the source of pollen, this lack of knowledge of individual parent trees will not seriously affect the application of results. Knowledge of the adaptability of trees grown from seed introduced from different localities is in itself a considerable contribution to the improvement of reforestation practice.

The existence of climatic races of forest trees is most evident in species having wide distribution in latitude, longitude, and altitude. Shaw (*29*, *p. 23*) states that—

> "the range of variation is somewhat proportionate to change of climate. * * * The western species of North America, for instance, are much more variable than the eastern species, while in Mexico, a tropical country with snow-capped mountains, the variation is greatest."

Thus ponderosa pine is particularly appropriate for a study of racial influence, for it is probably the most widely distributed conifer of western North America and certainly occurs in as great a diversity of climates as any other. Its range, according to Sudworth (*30*) and Munns (*22a*), extends in latitude from 23° in Mexico to 51°30′ in British Columbia, and in longitude from 98° in Nebraska to 124° in California.

[3] It is desired to acknowledge contributions to this project by D. R. Brewster, who prepared the working plan and supervised the installations, J. A. Larsen and G. Kempff, who made early examinations and records, C. A. Wellner and G. M. Fisher, who made recent measurements, and the late L. G. Hornby, who gave valuable help and advice in organizing the current results.

Two broad forms of ponderosa pine have long been recognized by foresters and dendrologists (*16, 28, 30* [4])—the *scopulorum* form, occurring mainly east of the Continental Divide, and the *ponderosa* form, occurring west of the Divide. Some authorities have recognized the *scopulorum* form as a variety and some have given it specific status. In the present study such division of the species was disregarded and progenies were classified solely on the basis of evidence produced by the study.

CLIMATIC DATA OF THE LOCALITIES OF SEED ORIGIN

The various localities in which the ponderosa pine seed used in this study was collected are shown in figure 1. The climatic regions indicated were delimited chiefly on the basis of data on precipitation types given by Ward (*33*). The boundaries of these regions as shown must be regarded as approximations only. The South Pacific region is the only one not represented by any of the seed used. Each seed-source locality has been designated by the name of the national forest that contains it. Of the three localities on the Bitterroot Forest, at altitudes of 4,000, 5,000, and 7,200 feet, each has been treated separately and further designated by its elevation. Weather Bureau records were obtained for the stations nearest to and most representative of the individual localities of seed origin. Table 1 locates each point where seed was collected and gives details of the Weather Bureau stations at which the records were taken, and the periods of years represented by the records.

Mean annual and mean monthly precipitation was determined for each locality. These data are shown graphically in figure 2. Precipitation and temperature records are given in detail in table 2. Because precipitation and temperature in any locality vary with altitude, it was necessary in a few instances to make some adjustment for the considerable differences in altitude between place of seed origin and the nearest weather station. The adjustments made to render the records representative of these seed-collection sites are explained in the footnotes to the table. Table 2 further contains precipitation-effectiveness indices, showing the balance between evaporation and precipitation; the larger the values, the better the net result in plant growth.

Large variations in several factors are conspicuous as between the different localities. The lowest average annual precipitation was 13.05 inches, for Ashley, and the highest was 51.48 inches, for Siskiyou; the lowest July-August precipitation was 0.36 inch, for Siskiyou, and the highest was 8.83 inches, for Santa Fe.

Annual mean temperature was lowest (33.5° F.) for Bitterroot 7,200 feet and highest (50°) for Siskiyou. For January, the coldest month in every locality, Custer had the lowest mean, 16.8°, and Siskiyou the highest, 35°. The highest and lowest temperatures, 114° and −57°, were recorded in the same locality, Custer. The most equable climate is that of Siskiyou, where the extremes were 108° and −2°.

[4] Also a preliminary study (unpublished) of the western yellow pine made by H. M. Curran in 1905. In Forest Service files.

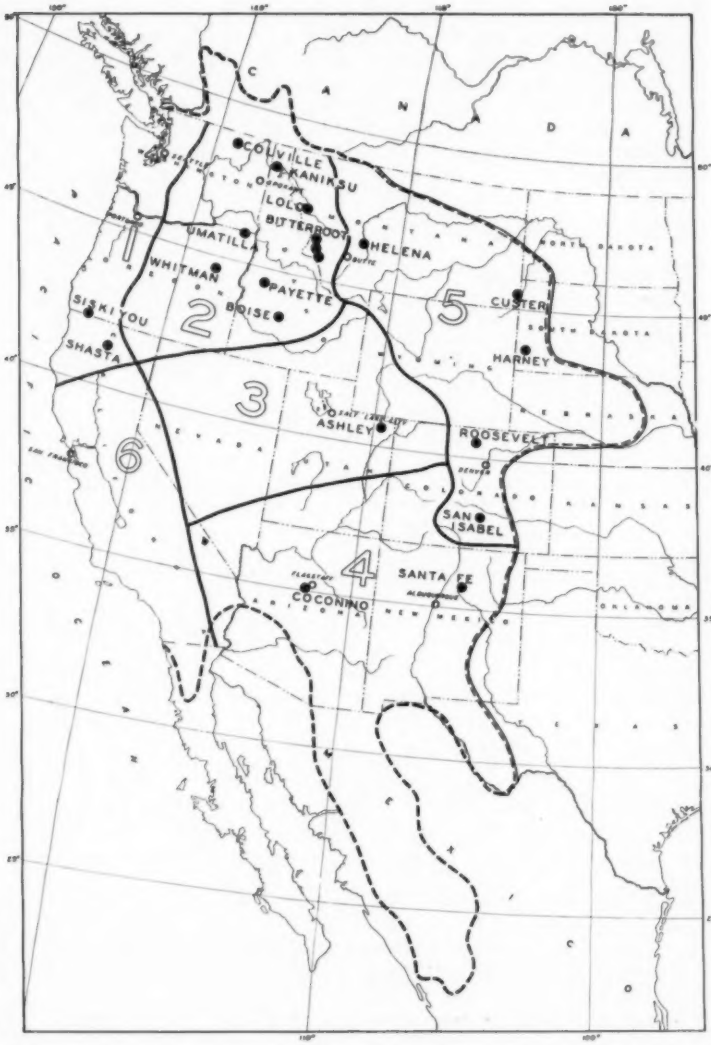


FIGURE 1.—Climatic regions of ponderosa pine range: (1) North Pacific; (2) north plateau; (3) central plateau; (4) south plateau; (5) east of Continental Divide; (6) South Pacific. The broken line shows the range of ponderosa pine according to Sudworth (*30*) and Munns (*22a*). Localities from which seed used in experiment was derived are indicated by black dots.

TABLE 1.—*Details of seed-collection points and corresponding weather-recording stations*

Location of seed-collection point [1]					Locus and extent of weather record				
Region and forest	Latitude	Longitude	Altitude		Locality	Altitude	Distance from seed source	Period of record	Length of record
North Pacific:	° ′	° ′	*Feet*			*Feet*	*Miles*		*Years*
Siskiyou	42 05	123 40	2,000		Waldo	1,650	5	1915–1935	16
Shasta [2]	41 30	122 20	4,000		McCloud	3,270	20	1911–1934	24
					Mount Shasta	3,555	15	1888–1934	47
North plateau:									
Boise	43 30	115 00	5,500		Soldier Creek	5,755	20	1910–1935	26
Payette	44 30	116 00	5,000		McCall	5,025	20	1905–1935	22
Whitman	44 38	118 25	5,000		Austin	4,200	4	1916–1935	11
Umatilla	46 00	117 30	3,500		Wallowa	2,935	28	1915–1935	21
Colville	48 40	119 00	2,700		Laurier	1,644	40	1910–1934	25
					Republic	2,628	10	1900–1934	29
Kaniksu	48 20	116 50	2,600		Priest River Experiment Station.	2,380	1	1912–1935	24
Lolo	47 10	114 50	3,000		Superior	2,975	3	1914–1934	19
Bitterroot	46 00	114 20	4,000 5,000 7,200		Como	3,750	5	1908–1921	14
South plateau:									
Coconino	35 10	111 50	7,100		Williams	6,750	20	1888–1934	35
					Flagstaff	6,907	20	1888–1934	44
					Fort Valley	7,300	25	1909–1934	22
					Rociada	7,150	25	1904–1926	23
Santa Fe	35 40	105 30	8,000		Gallinas Planting Station.	7,500	15	1907–1930	24
					Winsor's Ranch	8,000	25	1895–1935	40
East of Continental Divide:									
Helena	46 30	111 50	4,500		Helena	4,110	10	1880–1934	55
Custer	45 30	104 00	3,200		Camp Crook	3,103	10	1892–1935	42
Harney	43 40	103 30	5,000		Deadwood	4,535	40	1917–1930	14
					Custer	5,309	5	1911–1935	23
Roosevelt	40 30	105 40	8,000		Moraine	7,775	10	1890–1916	26
					Estes Park	8,000	5	1909–1934	26
San Isabel	38 00	105 00	8,000		Goodpasture	6,120	10	1917–1926	8
Central plateau:					Manila	6,225	20	1910–1934	25
Ashley	40 40	109 40	7,500		Elkhorn-Ashley	6,657	10	1910–1934	25
					Fruitland	7,000	50	1910–1929	20

[1] The localities are designated in the text by the names of the national forests containing them. The three localities on the Bitterroot National Forest are further designated by elevation. Seed was also collected on the Coeur d'Alene National Forest but proved to be valueless for this experiment since it comprised 2 distinct forms of ponderosa pine.

[2] All trees from this seed source were lost by freezing in 1924.

In considering the precipitation and temperature values in table 2 it should be borne in mind that these factors exert their influence on trees not independently but in combination, and that the altitude of the band on which ponderosa pine occurs increases from north to south, approximately at the rate of 350 feet for each degree of latitude.

Because of the many factors involved for which no exact data on degree of influence are available, it is evident that only general conclusions can be reached as to correspondence between climate and regional form of ponderosa pine. Furthermore, the number of parent localities represented in this study is too small to make possible a close definition of the range of any regional form.

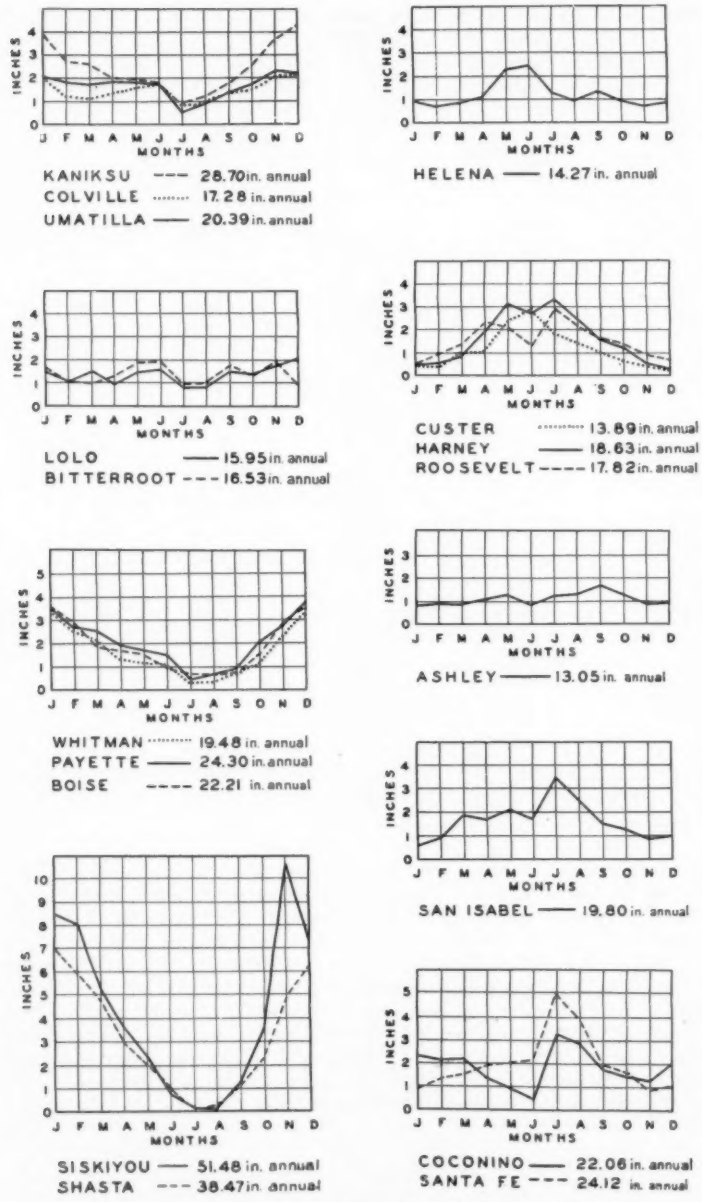

INCHES
MONTHS
J F M A M J J A S O N D
KANIKSU --- 28.70 in. annual
COLVILLE ..... 17.28 in. annual
UMATILLA —— 20.39 in. annual
HELENA —— 14.27 in. annual
LOLO —— 15.95 in. annual
BITTERROOT --- 16.53 in. annual
CUSTER ..... 13.89 in. annual
HARNEY —— 18.63 in. annual
ROOSEVELT ---- 17.82 in. annual
WHITMAN ..... 19.48 in. annual
PAYETTE —— 24.30 in. annual
BOISE ---- 22.21 in. annual
ASHLEY —— 13.05 in. annual
SISKIYOU —— 51.48 in. annual
SHASTA --- 38.47 in. annual
SAN ISABEL —— 19.80 in. annual
COCONINO —— 22.06 in. annual
SANTA FE --- 24.12 in. annual

FIGURE 2.—Precipitation types of localities of seed origin.

TABLE 2.—*Summary of weather records for localities of seed origin*

Region and forest	Average precipitation [1]				Minimum annual precipitation	Average temperature [2]			Extremes of temperature		Average date of first 40° F. daily mean	Precipitation-effectiveness indices [3]	Average frostless season [4]	Latest frost on record [4]	Earliest frost on record [4]
	Annual	April, May, and June	July and August	April–August, inclusive		Annual	April, May, and June	July and August	Highest	Lowest					
North Pacific:	*Inches*	*Inches*	*Inches*	*Inches*	*Inches*	°*F.*	°*F.*	°*F.*	°*F.*	°*F.*			*Days*		
Siskiyou	51.48	6.49	0.36	6.85	36.79	50.0	54.1	66.6	108	−2	Feb. 20	164.1	159	June 11	Sept. 3
Shasta	38.47	5.83	.42	6.25	21.33	47.0	51.3	63.7	106	−11	Mar. 20	138.0	108	July 6	Aug. 24
North plateau:															
Boise	22.21	4.10	1.25	5.35	13.45	42.3	48.8	65.1	100	−26	Apr. 15	85.0	78	July 30	Aug. 1
Payette	24.30	5.11	1.03	6.14	13.82	40.2	47.0	62.4	104	−46	Apr. 20	95.6	69	July 26	Aug. 4
Whitman	19.48	3.41	.61	4.02	12.61	39.0	46.1	58.7	101	−40	do	79.5			
Umatilla	20.39	5.44	1.49	6.93	10.60	43.3	50.3	62.9	106	−40	Apr. 1	65.4	110	June 30	Aug. 15
Colville	17.28	4.56	1.75	6.31	9.81	43.6	51.7	63.7	109	−35	do	52.9	88	July 14	Aug. 6
Kaniksu	28.70	5.52	1.87	7.39	16.02	43.3	50.8	63.2	102	−35	Apr. 5	104.9	62	July 27	Aug. 13
Lolo	15.95	4.06	1.57	5.63	7.61	44.9	52.1	66.0	104	−33	Mar. 25	46.5	103	July 1	Do.
Bitterroot:															
4,000 feet	16.53	5.05	1.95	7.00	13.58	44.2	51.4	64.0	103	−33	Apr. 1	45.4	127	June 8	Aug. 25
5,000 feet						41.0	48.2	60.8			Apr. 10				
7,200 feet						33.5	40.7	53.3			May 10				
South plateau:															
Coconino	22.06	2.83	6.20	9.03	11.79	45.4	50.7	64.1	102	−33	Apr. 5	62.6	110	July 29	Aug. 15
Santa Fe	24.12	6.04	8.83	14.87	14.84	42.9	48.1	59.4	92	−33	Apr. 15	59.0	116	July 21	Aug. 20
East of Continental Divide:															
Helena	14.27	5.80	2.10	7.90	7.38	42.2	50.3	65.2	102	−43	Apr. 10	36.1	145	June 9	Aug. 25
Custer	13.89	6.30	3.16	9.46	6.50	43.3	53.1	69.1	114	−57	do	28.5	120	June 20	Aug. 28
Harney	18.63	7.61	5.80	13.41	9.27	41.9	49.4	64.1	100	−31	do	41.3	112	June 17	Aug. 25
Roosevelt	17.82	5.68	4.90	10.58	11.08	41.4	46.6	59.8	98	−42	Apr. 25	48.1	91	July 20	Aug. 17
San Isabel	19.80	5.54	5.97	11.51	13.35	41.7	48.6	62.3	96	−36	Apr. 20	52.7			
Central plateau: Ashley	13.05	3.34	2.51	5.85	6.35	39.6	46.4	61.2	94	−36	Apr. 25	35.1	85	July 10	Aug. 25

[1] All the precipitation figures, except those for 4 localities, are exactly as shown by the basic weather-station data used. For the Whitman and Helena localities the weather-station records were increased 10 percent, and for the Umatilla locality they were increased 25 percent, to make them representative of the seed-collection points. This was done on the advice of the local forest officers, and by checking against precipitation maps of the Atlas of American Agriculture (*15*). For the Colville locality the local forest officer recommended use of the Laurier precipitation records as more representative than those of the more closely located Republic weather station. With these corrections, the figures approximate closely the precipitation of 16 of the localities of seed origin. The Ashley, San Isabel, Bitterroot 5,000 feet, and Bitterroot 7,200 feet seed-origin points are 843 to 3,450 feet higher than the local weather stations, and doubtless have somewhat greater precipitation than is shown here; but basic data are not available for correction.

[2] To make temperature figures of weather stations representative for seed-origin localities at greater altitudes, the customary reduction of 3.3° F. was made for every 1,000-foot difference in altitude.

[3] Precipitation-effectiveness indices for weather stations, computed by Thornthwaite's (*51*) method for integrating the effect of evaporation and precipitation.

[4] The frost figures are those of the weather stations, without adjustment. Except for the Umatilla, Bitterroot, Ashley, and Helena localities, it is believed that the frost conditions at the localities of seed origin are but slightly different from those at the weather stations.

EXPERIMENTAL AREA AND PLOTS

The experimental plantation is a part of the Priest River experimental forest of the Northern Rocky Mountain Forest and Range Experiment Station, located on the Kaniksu National Forest, in northern Idaho. It has an elevation of 2,380 feet. The climate is typical for the western white pine forest, with a mean annual precipitation of 28.70 inches, a moderately deep accumulation of snow, and a fairly heavy spring rainfall. July and August are characteristically hot and dry, with an average total of only 1.87 inches of rain and with prevailingly low relative humidity, which frequently goes below 15 percent. The annual mean temperature is 43.3° F., and frost may occur in any month.

The Kaniksu Forest is mainly occupied by the typical mixed stands of the western white pine type, composed principally of western white pine (*Pinus monticola*), western larch (*Larix occidentalis*), Douglas fir, lowland white fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Dry south slopes within the type often contain some ponderosa pine in mixture with the less moisture loving of the above species.

The progeny plots are situated in a clearing near the outer edge of a bench otherwise occupied by a natural second-growth stand in which larch and Douglas fir predominate over western white pine. A southwest slope that rises from the edge of the bench close to the plots has a natural open cover of ponderosa pine, larch, and Douglas fir. The bench has the appearance of an old river terrace. Lapham and Youngs [5] mapped the soil as Springdale sandy loam and described it as follows:

> The surface soil of the Springdale sandy loam is a friable fine to medium sandy loam, containing a small amount of gravel * * *. This material extends to a depth of 1 to 2 feet, * * * and overlies a subsoil of loose sand and gravel. This gravel is largely granitic and may be glacial outwash. The substratum, [which is] at a considerable depth, consists of old-lake clays.
>
> * * * The surface drainage is good and the subdrainage is generally excessive. The water-holding capacity is low due to thinness of the soil above the porous subsoil. This porous material also minimizes the upward movement of the capillary moisture. Altogether this is a droughty soil.

Small gravel pits were dug at three widely scattered points on the bench to a depth of 8 feet without exposing the clay substratum. The soil is very deficient in humus as a result of forest fires, which in about 1855 destroyed the virgin forest and some 40 years later destroyed a second-growth stand. A record made in 1917 stated that the soil retained moisture fairly well until about the middle of August, when it dried out to a moisture content of 3 or 4 percent of oven-dry weight at a depth of 12 inches, and then remained unchanged until the beginning of fall rains in September. Soil samples taken at a depth of 24 inches in the centers of all plots on August 31, 1936, had a moisture content ranging from 3 to 9 percent and averaging 4.7 percent. Recent soil-acidity tests made at three points on the planted area showed pH values ranging from 6.2 to 6.8. Rather too well drained for western white pine, the site of the plots appears from the growth rate and vigor of the planted trees to be well suited for ponderosa pine.

[5] LAPHAM, M. H., and YOUNGS, F. O. SOIL SURVEY OF THE PRIEST RIVER FOREST EXPERIMENT STATION. 1925. [Unpublished manuscript.]

As site conditions are practically uniform on the cleared part of the bench, and as the progeny plots form a small, compact block only 200 by 260 feet in size, the plots may be said to have closely comparable growing conditions. Because the foot of a slope touches the northeast corner of the plantation, however, three plots (the Bitterroot 7,200 feet, the Lolo, and the Bitterroot 4,000 feet) might be assumed to have an advantage as to soil moisture. As the slope has a southwest exposure, however, and the short distance to the ridge top precludes retention of any great amount of water, the advantage if any is not marked. Actual tests showed the Lolo and Bitterroot, 4,000 feet, plots to have slightly less soil moisture than the average for all the plots.

Although the crown canopy on some of the plots has become dense enough to shade out low vegetation in spots, most of the ground surface is still covered with herbaceous and shrubby vegetation of vary-

<table>
<tr><td>Payette
June 5, 1912</td><td colspan="2">Coconino
May 10, 1912</td><td>Santa Fe
May 3, 1915</td><td>Lolo
May 2, 1916</td><td>Bitterroot
7,200 feet
May 29, 1917</td></tr>
<tr><td>Coeur d'Alene
Oct. 6, 1911
(excluded)</td><td colspan="2">Custer
Oct. 6, 1911</td><td>Ashley
May 13, 1915</td><td>Kaniksu
May 2, 1916</td><td>Bitterroot
4,000 feet
May 31, 1917</td></tr>
<tr><td>Helena
Oct. 14, 1911</td><td>San Isabel
Oct. 14, 1911</td><td>Roosevelt
June 5, 1912</td><td>Bitterroot
5,000 feet
May 13, 1915</td><td>Siskiyou
May 3, 1916</td><td>Harney
May 2, 1916</td></tr>
<tr><td>Shasta
May 13, 1915
(excluded)</td><td>Umatilla
Nov. 18, 1911</td><td>Whitman
May 13, 1916</td><td>Boise
May 13, 1915</td><td>Colville
May 13, 1915</td><td>Unknown
Origin
April 29, 1916
(excluded)</td></tr>
</table>

FIGURE 3.—Arrangement of progeny plots, and dates of first planting. The large plots are 50 by 50 feet and the small ones 25 by 50 feet.

ing density. The most abundant species are *Arctostaphylos uva-ursi*, composing 25 to 75 percent of the low vegetation, and *Calamagrostis rubescens*, composing 10 to 65 percent. Other characteristic species, in the order of their abundance, are *Fragaria glauca*, *Pentstemon* sp., *Achillea lanulosa*, *Symphoricarpos racemosus*, *Odostemon aquifolium* (syn. *Berberis aquifolium*), *Pteridium aquilinum pubescens*, and *Ceanothus velutinus*. All these species are typical of the drier sites in this locality.

The progeny trees representing each locality of seed origin were planted on 1 of the 22 plots shown in figure 3. On each of the 18 large plots, 50 feet square, 100 trees were planted, and on each of the 4 small ones, 25 by 50 feet, 50 trees were planted. Spacing of trees was exactly 5 by 5 feet.

The stock used in the first 8 plot installations, made in the fall of 1911 and the spring of 1912, and in 3 made in 1913, 1915, and 1916, was grown in Forest Service nurseries in various regions. For the 11 other installations, made in 1915, 1916, and 1917, stock was grown in a small nursery at the site of the experiment. The trees were planted

on the plots as 2- and 3-year-old transplants. The method was to dig an open hole, spread the roots around a mound of earth in the center, and firm the soil by hand.

For 3 to 5 years after each first installation, all trees that died were replaced with trees of the same lot that had been reserved in the nursery, in order to maintain closed-stand conditions.

Of the 22 progenies shown in figure 3, only 19 are treated in this report. All the trees on the Shasta plot were lost by freezing in 1924. Because its seed-source record is very questionable, the plot designated "Unknown origin" was omitted. The plot designated "Coeur d'Alene" has a mixture of two distinct forms of ponderosa pine and was therefore excluded also.

Every year from 1912 to 1919, the plots were examined and a record was made of the number of living and dead trees, the number of replacements, and the height of a representative 20 percent of the trees on each plot. Similar records including heights of all trees were made in 1927 (*14*). In 1935, measurements of height and diameter were made on all the trees, and also of internode lengths of the main stem for the years 1930–35. Records were made, also, of survival, vigor, dominance, and foliage characteristics.

FOLIAGE CHARACTERISTICS

The foliage of each progeny was classified as to number of needles per fascicle, length of needles, number of years needles were retained, general appearance of foliage, and internal structure of needles. In this connection it should be kept in mind that the progenies are about the same age, are situated close together on level ground practically uniform as to soil and moisture, and are uniformly exposed to sun and wind.

NUMBER OF NEEDLES IN FASCICLE

In discussing the pines, Shaw (*29, p. 4*) says:

> The number of leaves in the fascicle is virtually constant in most species, the variations being too rare to be worthy of consideration. With some species, however, heteromerous fascicles are normal. The influences that cause this variation are not always apparent (*echinata*, etc.), but with *P. ponderosa*, *leiophylla*, *sinensis*, and others, the number of leaves in the fascicle is, in some degree, dependent on climatic conditions, the smaller number occurring in colder regions.

The fascicles of *Pinus ponderosa*, Shaw states, consist prevailingly of three needles each, but range from two to five or more, the larger numbers occurring in the southern part of the tree's range.

In the progenies of this experiment the number of needles to the fascicle varied from two to three. To determine the proportions of two- and three-needle fascicles, an examination was made of the foliage of 20 trees on each of the progeny plots. On each of these trees 10 fascicles were examined on each of 5 branches selected at random from the lower half of the crown. On each branch, approximately equal numbers of fascicles were examined on each of the internodes having green needles. A separate record was kept for each tree. For each plot the average percentage of fascicles containing three needles was determined, as shown in table 3.

Comparison of progeny trees with native trees as to the proportion of three-needle fascicles was made by the use of specimen branches obtained from the parent localities. As the foliage in any locality

may vary greatly among individual trees according to age of tree, exposure, and character and moisture content of the soil, and on a single tree according to position in the crown, collectors were requested to select outer branches below the middle of the crown on the south sides of vigorous trees, 20 to 40 years old, growing in open stands on good sites. Thus an effort was made to obtain foliage specimens from the same general position in the crown and from the same kinds of trees as on the progeny plots. From 3 to 10 specimens, representing that number of trees, were obtained from each locality. On each branch 50 fascicles were examined, a total of 150 to 500 for each locality. The results are presented in table 3.

TABLE 3.—*Percentage of fascicles containing three needles,*[1] *on progeny plots and in parent localities*

Climatic region and locality of seed origin	Fascicles containing 3 needles		Group character
	Progeny plot	Parent locality	
	Percent	*Percent*	
North Pacific: Siskiyou	93	100	Typically 3-needled.
North plateau:			
Boise	95	99	
Payette	97	100	
Whitman	98	93	
Umatilla	98	100	
Colville	93	100	
Kaniksu	93	94	
Lolo	95	99	
Bitterroot:			
4,000 feet	97	95	
5,000 feet	94	98	
7,200 feet	95	99	
South plateau:			
Coconino	94	97	
Santa Fe	92	96	
East of Continental Divide:			
Helena	69	88	Intermediate.
Custer	24	25	Typically 2-needled.
Harney	24	7	
Roosevelt	11	22	
San Isabel	51	43	
Central plateau: Ashley	60	76	

[1] All fascicles not containing 3 needles contained 2.

In all cases, the findings for trees in a parent locality and those for the progeny derived from that locality were similar, indicating that number of needles to the fascicle is an inherited characteristic persisting at least through the first 22 to 26 years of the progeny's life. The evidence from the areas sampled shows that in general three-needle fascicles are characteristic of ponderosa pine in the north and south plateau regions and two-needle fascicles are characteristic east of the Continental Divide. The Helena locality, close to the Divide on the east, is an exception. The Ashley locality, in the central plateau region, tends to be intermediate.

LENGTH AND PERSISTENCE OF NEEDLES

With regard to variation in needle length, Shaw (*29, p. 4*) says:

> Among conifers, the leaf of Pinus attains extraordinary length with great variation, * * * the maximum for each species being usually much more than twice the minimum. Climate is the predominating influence; for the shortest leaves occur on alpine and boreal species, the longest leaves on species in or near the tropics.

The length of the leaf is complicated by the peculiarities of individual trees and by pathological influences; as a general rule, however, the length of leaves is less or greater according to unfavorable or favorable conditions of temperature, moisture, soil and exposure. Therefore the dimensions of the leaf may be misleading. It can be said, however, that certain species always produce short leaves, others leaves of medium length, and others very long leaves.

Data on needle length were collected not only on progeny trees but also on trees in the parent localities. The method of selection was to pluck at random 10 or more fascicles from 1 branch on each of 3 trees, taking a proportionate number from each of the internodes. Measurements were made of 30 or more needle clusters for each progeny plot, and 50 for each parent locality. Average length was calculated for the shortest 10 and the longest 10 to obtain "principal range," and for the total number of fascicles.

TABLE 4.—*Length of needles on progeny plots and in parent localities*

Climatic region and locality of seed origin	Progeny plot		Parent locality		Group character
	Principal range	Average	Principal range	Average	
	Inches	*Inches*	*Inches*	*Inches*	
North Pacific: Siskiyou	4.8–6.6	5.9	4.9–7.6	6.4	Long.
North plateau:					
Boise	4.8–6.5	5.8	4.8–7.5	6.1	
Payette	4.4–6.8	5.6	4.4–6.6	5.7	
Whitman	4.2–6.9	5.9	4.8–6.7	5.9	
Umatilla	4.7–6.6	5.8	5.4–7.9	6.9	
Colville	4.7–5.8	5.4	5.1–6.6	5.7	
Kaniksu	4.7–6.2	5.6	5.0–7.1	6.0	
Lolo	5.8–6.8	6.3	5.1–7.1	6.1	
Bitterroot:					
4,000 feet	4.9–7.4	6.1	5.1–6.8	6.1	
5,000 feet	4.3–6.7	5.6	3.5–6.3	4.8	
7,200 feet	4.0–5.9	5.0	3.7–6.0	5.0	
South plateau:					
Coconino	4.0–5.8	4.9	4.5–6.2	5.4	Medium to long.
Santa Fe	3.9–5.3	4.6	4.7–7.6	6.2	
East of Continental Divide:					
Helena	3.9–5.7	4.9	5.8–7.6	6.7	
Custer	3.0–4.2	3.7	4.4–6.8	5.7	
Harney	2.7–3.9	3.4	3.2–5.3	4.3	
Roosevelt	2.9–4.7	3.8	3.2–4.8	4.1	Short.
San Isabel	3.2–5.0	4.2	4.2–6.0	5.2	
Central plateau: Ashley	3.2–5.2	4.3	3.2–5.2	4.2	

It appears from the data in table 4 that characteristics as to needle length were hereditary in the progenies studied, at least for the first 22 to 26 years of their lives; that is, that for 20 years and more the progeny have for the most part fallen into the same general classifications of long, medium, and short needles as did the trees in the parent localities. The data show that the needles of trees of the North Pacific and north plateau regions are long, that those of the south plateau are medium to long, and that those of the central plateau and of the localities east of the Continental Divide are short. The Helena trees are again an exception, their needles being medium to long, more like those of localities west of the Divide.

Data on persistence, or the number of years needles remain green on the tree, were obtained for the progeny plots by recording for each of 5 branches on 20 trees per plot the number of internodes having green needles. Corresponding data for trees of the parent localities

were obtained by examining all the specimen branches collected in each locality. These data are presented in table 5.

TABLE 5.—*Number of years needles persist on progeny plots and in parent localities*

Climatic region and locality of seed origin	Progeny plot		Parent locality	
	Principal range	Mode [1]	Principal range	Mode [1]
	Years	*Years*	*Years*	*Years*
North Pacific: Siskiyou	2-4	3	2-3	3
North plateau:				
Boise	3-4	3	4-5	4
Payette	3-4	3	4-5	4
Whitman	3-4	3	[2] 4-6	[2] 5
Umatilla	3-4	3	5-6	6
Colville	3-4	4	4-5	5
Kaniksu	3-4	4	4-5	5
Lolo	3-4	3	4-5	5
Bitterroot:				
4,000 feet	3-4	4	4-5	4
5,000 feet	3-4	4	4-5	4
7,200 feet	3-4	3	4-5	4
South plateau:				
Coconino	3-4	3	[2] 4-7	[2] 6
Santa Fe	3-4	3	([3])	([3])
East of Continental Divide:				
Helena	3-4	3	4-5	5
Custer	3-4	4	4-6	5
Harney	3-4	4	3-4	4
Roosevelt	3-4	4	5-7	6
San Isabel	3-4	3	4-6	6
Central plateau: Ashley	3-4	3	6-9	8

[1] The value occurring in the greatest number of cases.
[2] Values estimated on basis of incomplete evidence.
[3] Evidence available too incomplete to serve as basis for estimate.

Persistence is closely related to needle length. In general, where the growing season is short and rigorous, as at high altitudes, both shoots and needles are short. To compensate for this dual dimensional deficiency, needles must persist on more internodes than under more favorable conditions. Examples of high-altitude species having short needles persisting over a long period are *Pinus albicaulis* and *P. balfouriana*.

Needles persisted mainly 4 or 5 years in parent localities in the north plateau region, 6 years in the more severe Roosevelt and San Isabel localities, and 8 years in the rigorous Ashley locality; but needles on the progeny trees uniformly persisted only 3 or 4 years, regardless of origin. Thus it appears that, in ponderosa pine, needle persistence is not inherited, and that if the same area of leaf surface is maintained in the Priest River as, for example, in the Ashley environment this is done in some other way than by long retention of needles. The method of adjustment in this particular case is indicated by the fact that the length of the three internodes containing green needles on Ashley progeny trees averaged practically the same as the length of the eight internodes containing green needles on Ashley parent-locality trees.

It is interesting to note that in experimental plantations in Switzerland containing trees of different seed origin, Burger (*5*) and Nägeli (*23*) found needle persistence of Scotch pine and Norway spruce, respectively, to be uniform regardless of shorter or longer retention in different parent localities.

INTERNAL STRUCTURE OF NEEDLES

In order to ascertain what differences in needle structure exist among the progenies of this experiment, arrangement was made with J. H. Ramskill, professor of forestry in the University of Montana, to undertake cooperatively a microscopic study of the needles. Professor Ramskill was supplied with needles from each progeny plot and from each parent locality, collected according to methods of sampling already described. He made a great number of cross sections from these needles, studied 688 of them, and made photomicrographs of selected sections. Some of the structural characteristics found by Ramskill to be most consistent and most clearly heritable are here summarized.

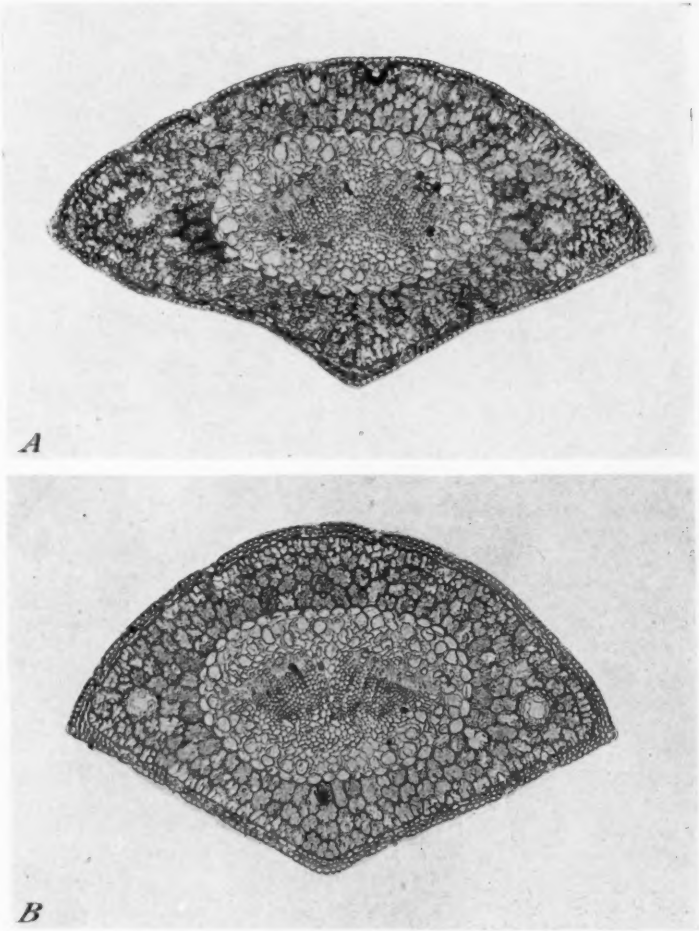
Leaf features in which plants are known to make protective adjustments in different habitats are thickness of hypoderm and character of stomatal chambers. The hypoderm in ponderosa pine is biform, having an outer row of cells (next to the epidermis) which is always thin-walled and an inner row or several inner rows of cells which may be thick-walled or thin-walled. In localities of severe climate, the inner rows may be many and composed solidly of thick-walled cells; in localities of moderate climate, they may be fewer in number and composed of thick-walled and thin-walled cells interspersed; in localities of mild climate there may be only one or two inner rows composed mainly of thin-walled cells, with a few interspersed thick-walled cells.

The observed extremes in these features are shown in plates 1, 2, and 3. It is readily seen in these photomicrographs that the hypodermal layer is composed of only a few rows of cells in needles from the Siskiyou locality, which has a mild climate, and of many rows in needles from the Ashley locality, which has a severe climate. Similarly the former are seen to have little depression of the stomata, whereas the latter have deeply depressed stomata. It is evident that the degree to which the openings of stomatal chambers are sunk below the general level of the leaf surface corresponds to the number of rows of cells in the hypoderm. Table 6 presents data on these two characteristics.

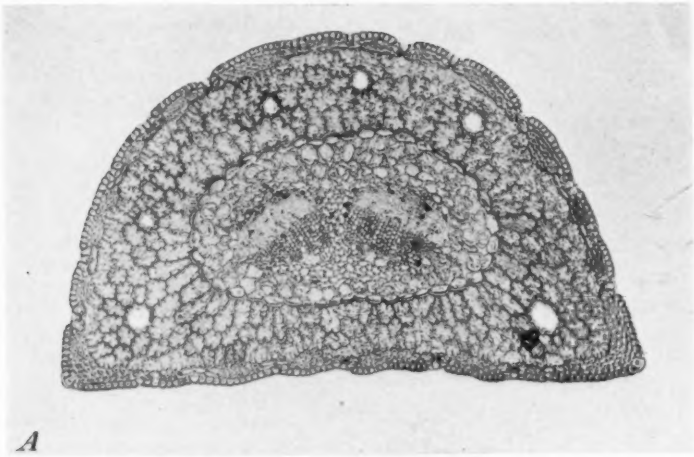
From the table and the plates it appears that, in general, hypoderm-cell and stomatal-depression characteristics have been inherited by the progenies in the new habitat and retained by them. A slight variation in degree of inheritance seems to be indicated in progenies derived from localities in the south plateau region and east of the Continental Divide, which have climates more rigorous than that of the experimental site on the Kaniksu Forest. Needles of these progenies tend to have somewhat fewer rows of hypoderm cells and slightly less stomatal depression than do needles in the parent localities.

When the localities are grouped by similarity of the hypodermal and stomatal characteristics described, as in table 6, they fall into three distinct main groups: (1) The North Pacific locality by itself, (2) the north plateau localities, and (3) all the localities of the central and south plateaus and the region east of the Continental Divide. Again the Helena locality is intermediate, resembling the north plateau localities more than the others.

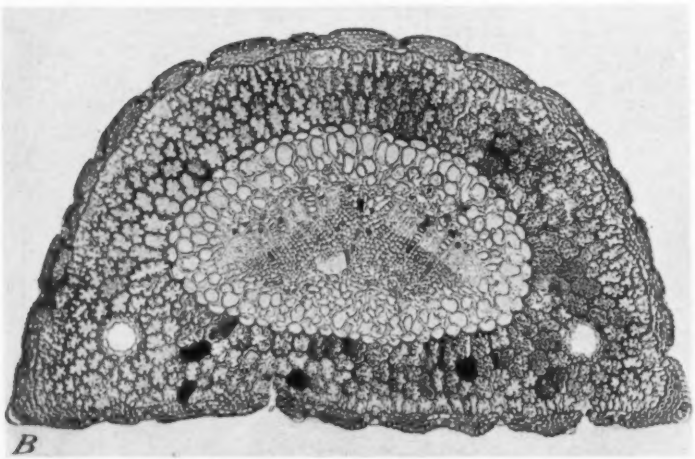
Table 7 presents data on two other features of needle structure—relative thickness of walls in inner rows of hypoderm cells and percentage of thick-walled cells in inner hypoderm rows. According to the available evidence, each of these characteristics may be regarded as inherited.



Cross sections of needles of Siskiyou trees, showing thin layer of hypoderm cells and little stomatal depression: *A*, Needle from parent locality; *B*, needle from progeny plot. Note the similarity between *A* and *B*, indicating inheritance of these characteristics in the new environment. These specimens are typical of the foliage of Siskiyou trees and closely resemble specimens typical of the foliage of north plateau trees. × 110.



A



B

Cross sections of needles of Ashley trees, showing thick layer of hypoderm cells and deeply depressed stomata: *A*, Needle from parent locality; *B*, needle from progeny plot. Note the similarity between *A* and *B*, indicating inheritance of these characteristics in the new environment. These specimens are typical of the foliage of trees of the region east of the Continental Divide and the central and south plateau regions. × 110.

TABLE 6.—*Number of inner rows of hypoderm cells containing thickened cell walls and depression of stomata in needles on progeny plots and in parent localities*

Climatic region and locality of seed origin	Inner rows of hypoderm cells containing thickened cell walls		Depression of stomata		Group characteristics	
	Progeny plot	Parent locality	Progeny plot	Parent locality	Rows containing thickened cell walls	Depression of stomata
	Number	*Number*				
North Pacific: Siskiyou	1, 2	1, 2	None	None	Few	None.
North plateau:						
Boise	1, 2, 3	1, 2, 3	Moderate	None, moderate.		
Payette	1, 2, 3	1, 2, 3	do	do		
Whitman	1, 2	1, 2, 3	None, moderate.	do		
Umatilla	1, 2	1, 2, 3	Moderate	do		
Colville	1, 2	1, 2, 3	None, moderate.	do		Slight to moderate.
Kaniksu	1, 2	1, 2	do	do	Few to moderate.	
Lolo	1, 2, 3	1, 2	do	Moderate		
Bitterroot:						
4,000 feet	1, 2	1, 2, 3	do	do		
5,000 feet	1, 2, 3	1, 2	Moderate	None, moderate.		
7,200 feet	2, 3	1, 2	do	do		
East of Continental Divide:						
Helena	1, 2, 3	1, 2, 3	do	Moderate, deep.		Moderate to deep.
Custer	2, 3, 4	3, 4, 5	Deep	do		
Harney	2, 3, 4	2, 3, 4	do	Deep		
Roosevelt	2, 3, 4	3, 4, 5	do	do		
San Isabel	1, 2, 3, 4	2, 3, 4, 5	do	do		
South plateau:					Many	Deep.
Coconino	2, 3	3, 4, 5	do	do		
Santa Fe	2, 3, 4	3, 4	do	Moderate		
Central plateau: Ashley	2, 3, 4, 5	2, 3, 4, 5	do	Deep		

TABLE 7.—*Relative thickness of walls in inner rows of hypoderm cells and proportion of thick-walled cells in hypoderm of needles on progeny plots and in parent localities*

Climatic region and locality of seed origin	Relative thickness of cell walls [1]		Proportion [2] of hypoderm cells having thick walls		Group characteristics	
	Progeny plot	Parent locality	Progeny plot	Parent locality	Cell-wall thickness	Cells having thick walls
North Pacific: Siskiyou	I, II	I	F, M	F, M	Mostly thin	Few.
North plateau:						
Boise	II	I, II	M, A	M, A		
Payette	I, II, III	I, II	M, A	M		
Whitman	I, II, III	I, II	M	M, A		
Umatilla	I, II, III	I, II	M	A		
Colville	I, II	I, II	M	M		
Kaniksu	I, II	I, II	M	M, A	Mostly thin to thick.	Moderate to many.
Lolo	I, II	I, II	M	A		
Bitterroot:						
4,000 feet	I, II	II	M	M, A		
5,000 feet	II	II	M	M, A		
7,200 feet	II	II	M, A	M, A		
East of Continental Divide:						
Helena	II, III	II	M, A	M, A	Mostly thick.	
Custer	II, III	II, III	A	M, A		
Harney	II, III	II, III	A	A		
Roosevelt	II, III	II, III	A	A		
San Isabel	II, III	II, III	A	A	Thick to very thick.	Practically all.
South plateau:						
Coconino	II, III	II, III	A	A		
Santa Fe	II, III	II, III	A	M, A		
Central plateau: Ashley	II, III	II, III	A	A		

[1] I=thin, or only slightly thicker than cell walls of epidermis; II=thick, or conspicuously thicker than cell walls of epidermis; III=very thick, or so thick as almost to eliminate lumen.

[2] As determined along perimeters of cross sections of needles. Includes all cells having thick or very thick walls. F=0–50 percent; M=51–99 percent; A=all, or 100 percent.

It will be noted that the localities fall into the same three groups on the basis of these characteristics as of those in table 6, and that the Helena locality is intermediate here also, with closer resemblance to the north plateau localities than to the others east of the Continental Divide.

GENERAL APPEARANCE OF FOLIAGE

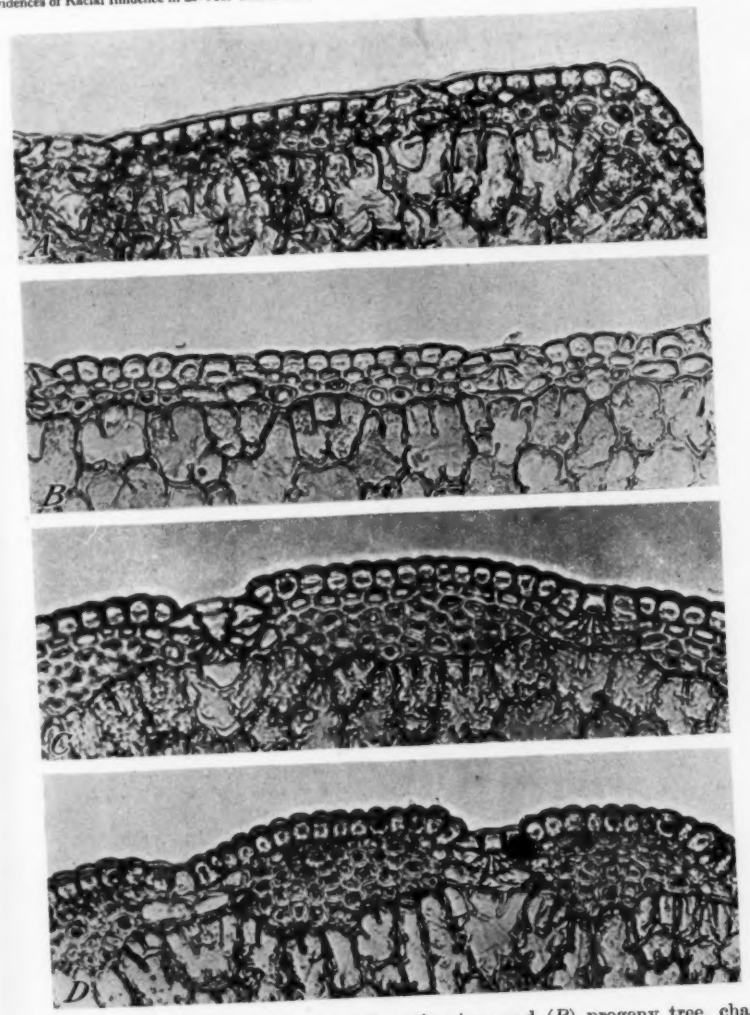
Even casual observers of the progeny plots have noticed many differences among the various progenies in general appearance of foliage. Corresponding differences are observed among the trees of the parent localities. The typical foliage appearance of the North Pacific and north plateau progenies is exemplified by the Umatilla progeny, illustrated in plate 4, *A*, and that of the progenies from east of the Continental Divide and from the central plateau by the Roosevelt progeny, illustrated in plate 4, *B*. Trees of the former group have relatively long, slender, flexible needles, typically occurring in fascicles of three, arranged on the branches in rather open plumes. Those of the latter have stiff, short, coarse needles, typically occurring in fascicles of two,[6] arranged more compactly on the branches and in many cases curved toward the stem. The foliage appearance of the south plateau progenies, illustrated in plate 4, *C*, is intermediate.

Thickness and stiffness of the needles are roughly proportional to quantity of stiffening tissue in the hypoderm, data on which are shown in tables 6 and 7. The foliage of the Coconino and Santa Fe stocks, in spite of heavy strengthening of the hypoderm, has an open appearance as compared with that of progenies or native trees of either the central plateau or the region east of the Continental Divide. This is accounted for by moderate length and relative slenderness of needles.

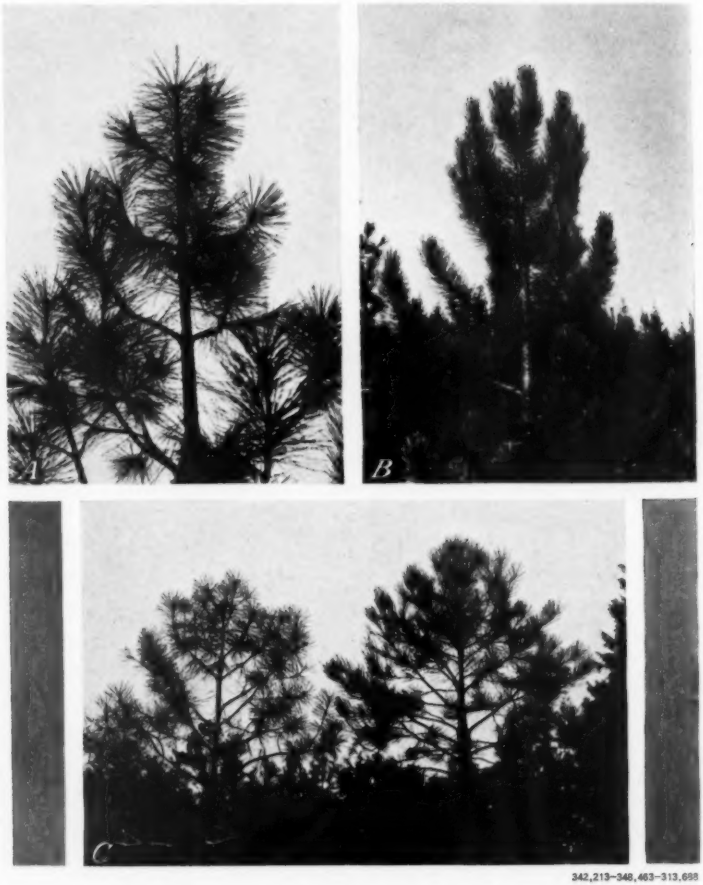
It is difficult to make distinctions as to color of foliage, because color is elusive and apparently varies to some degree with season, site, and health of the tree, and because the current year's foliage is often brighter in hue than the older foliage. In general, as seen from a distance, the foliage of the North Pacific and north plateau progenies is medium green to slightly yellow green and that of the progenies from east of the Continental Divide and from the central and south plateaus is gray green. On the basis of Ridgway's color charts (*26*), the progenies' foliage on the internode of the current season was classified in August 1936 as follows: Spinach green—Siskiyou, Kaniksu, Lolo, Bitterroot 4,000, Bitterroot 5,000, Bitterroot 7,200, Boise, Payette, Whitman, Umatilla, Colville, Coconino, Santa Fe, and Helena; light elm green—Roosevelt, Harney, Custer, and San Isabel; biscay green—Ashley. On the same basis their foliage on the internodes of earlier seasons was classified at that time as follows: Varney's green—Siskiyou, Kaniksu, Lolo, Bitterroot 4,000, Bitterroot 5,000, Bitterroot 7,200, Boise, Payette, Whitman, Umatilla, and Colville; deep dull yellow green—Coconino, Santa Fe, and Helena;

[6] The Ashley progeny in this group, with only 39.8 percent of its fascicles containing two needles, may still be said to be strongly two-needled in character. In contrast, in all the progenies classified as three-needled, the fascicles containing two needles amount to less than 8 percent.

PLATE 3



Sections of needles from Siskiyou (*A*) native tree and (*B*) progeny tree, characteristically containing few rows of hypoderm cells, and sections of needles from Ashley (*C*) native tree and (*D*) progeny tree, characteristically containing many rows of hypoderm cells. × 650.



342,213–348,463–313,698

Foliage characteristics of progenies: *A*, Open, plumelike arrangement of long, slender needles of Umatilla progeny, typical of the north plateau and north Pacific regions; *B*, compact, brushlike arrangement of short, thick needles of Roosevelt progeny, typical of the region east of the Continental Divide and the central plateau region; *C*, intermediate foliage characteristic of Santa Fe progeny, typical of the south plateau region.

pois green—Roosevelt, Harney, Custer, and San Isabel; light elm green—Ashley. A general correspondence in color was observed between trees of parent localities and progenies.

A purple bloom was found on tree branches collected in the Coconino and Santa Fe localities. On the progeny plots, in northern Idaho, a similar bloom appeared on twigs of Santa Fe, San Isabel, and Ashley trees but was not observed on Coconino trees.

GROUPING ACCORDING TO FOLIAGE CHARACTERISTICS

It is evident from the data presented in tables 3–7 that the localities of seed origin having similar foliage characteristics fall into a few groups, and that these groups are closely related to the climatic regions shown in figure 1. Table 8 summarizes these data.

It will be noted from table 8 that trees with preponderantly three-needle fascicles and long or moderately long, slender, flexible needles are found in the North Pacific, north plateau, and south plateau regions. Readily recognized differences in hypoderm structure, reflecting climatic differences, cause this group to subdivide into its three regional parts; hypoderm tissue is little or not at all thickened in the North Pacific trees, moderately thickened in the north plateau trees, and heavily thickened in the south plateau trees.

Trees having a preponderance of two-needle fascicles and distinctly short, thick, stiff needles with heavily thickened hypoderm tissue are typical of the region east of the Continental Divide.

In the Ashley and Helena localities foliage is intermediate in character. Needles of Ashley trees, in the central plateau region, are short, thick, and stiff and have heavy hypoderm structure, like those of trees east of the Divide. The central plateau trees resemble the south plateau trees in having more three-needle than two-needle fascicles. All factors considered, however, they are more closely related to those east of the Divide. The foliage of Helena trees is intermediate in needle length and hypoderm structure between typical foliage east of the Divide and that on the north plateau, but the similarity to the latter is much closer. This together with strong three-needle fascicle occurrence aligns the Helena trees with those of the north plateau. The Helena locality is only 15 to 20 miles east of the Divide, near enough to be affected by west side conditions.

Although no progenies from the South Pacific region are represented in this experiment, foliage data are available from specimen branches obtained from four trees at Quincy, in north central California. Collection and study of the branch material followed the procedure described for studying the foliage characteristics of trees in parent localities. The foliage of the Quincy trees had 99 percent of three-needle fascicles, and long, slender, flexible needles. Average length of needles was 7.3 inches, and principal range was 6.6 to 8.1 inches, longer than any measured in the experiment. Inner rows of hypoderm cells containing thickened tissue were few to moderate in number, the cell walls were only slightly to moderately thick, and stomata were but slightly to moderately depressed. All these characteristics are typical of the trees of the North Pacific and north plateau regions.

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TABLE 8.—*Summary of foliage characteristics by regions, based on progeny trees and trees in parent localities*

Region or locality of seed origin	Typical appearance of foliage	Fascicles		Needle length			Hypodermal thickening
		General type	Having 3 needles	General type	Principal range	Average	
			Percent		*Inches*	*Inches*	
North Pacific	Needles long, slender, flexible. Foliage plumelike. Medium green to yellow green.	Typically 3-needled	90–100	Long	4.8–7.6	6.2	Very little.
North plateau	do	do	90–100	do	4.6–6.9	5.8	Moderate.
Helena	do	do	70–90	Medium to long	3.9–7.6	5.8	Moderate to heavy.
South plateau	Needles moderately long and slender, slightly stiff. Gray green.	do	90–100	do	4.0–6.9	5.4	Heavy.
East of Divide	Needles short, thick, stiff. Foliage bristly. Gray green.	Typically 2-needled	10–50	Short	2.9–5.7	4.3	Do.
Central plateau	do	Intermediate	60–75	do	3.2–5.2	4.2	Do.

GROWTH CHARACTERISTICS

HEIGHT AND DIAMETER OF PROGENY

The period from the first planting on a given progeny plot to the most recent measurement of the trees, in 1935, varied from 19 to 24 years. In order to compare all the progenies at a uniform age, heights and diameters were computed as of the end of the twentieth season after outplanting. As the nursery stock was in some cases 2 years and in others 3 years old at the time of outplanting, the total ages from seed represented by the height and diameter values thus obtained are 22 and 23 years.

In drawing conclusions from the growth figures, allowance should be made for the influences of density and spacing. All the plots are reasonably comparable in these respects except the Siskiyou, Bitterroot 7,200 feet, and Santa Fe, on which relatively few trees remain and these are widely spaced. As the surviving trees are the best of the individuals planted, at least on the first two plots, their growth is probably somewhat too advanced to be representative.

Table 9 shows for each plot the average height, the standard deviation of heights, and the extremes of height. Despite the uniformity of the site on which the trees are growing, there are wide differences in height growth. Average heights range from 15.7 feet for the Lolo to 7.2 feet for the Ashley progeny. In general the progenies derived from localities near the site of the experiment have made the best height growth. Those derived from the highest altitudes have in general made the least growth. These results are in agreement with those of European investigations (*5, 8, 9, 12, 35*).

TABLE 9.—*Height of progeny trees after 20 years' growth on plots* [1]

Region, locality, and altitude (feet) of seed origin	Average	Standard deviation	Standard error	Maximum	Minimum	Basis, trees
	Feet	*Feet*	*Feet*	*Feet*	*Feet*	*Number*
North Pacific: Siskiyou (2,000)	11.9	±4.5	±0.95	19.5	4.0	22
North plateau:						
Boise (5,500)	10.4	±4.2	±.50	27.5	3.0	71
Payette (5,000)	10.5	±2.7	±.40	19.0	3.5	45
Whitman (5,000)	9.4	±3.7	±.65	20.0	4.0	33
Umatilla (3,500)	11.7	±3.4	±.56	19.0	3.5	37
Colville (2,700)	12.4	±4.1	±.44	21.0	4.5	86
Kaniksu (2,600)	12.6	±3.9	±.50	21.0	1.5	61
Lolo (3,000)	15.7	±4.9	±.54	26.0	6.5	81
Bitterroot:						
4,000	14.5	±4.1	±.51	22.0	6.0	65
5,000	13.1	±3.7	±.40	23.0	2.5	86
7,200	11.4	±4.6	±.76	21.0	3.5	36
East of Continental Divide:						
Helena (4,500)	12.8	±3.4	±.36	21.0	6.0	87
Custer (3,200)	9.8	±3.0	±.35	15.5	4.0	70
Harney (5,000)	11.1	±4.9	±.55	17.0	4.0	79
Roosevelt (8,000)	8.6	±2.6	±.50	15.5	5.0	27
San Isabel (8,000)	9.0	±2.8	±.47	15.0	4.5	36
South plateau:						
Coconino (7,100)	9.0	±2.6	±.33	15.5	4.5	63
Santa Fe (8,000)	7.5	±2.4	±.54	11.0	3.0	20
Central plateau: Ashley (7,500)	7.2	±2.6	±.37	12.0	1.5	49

[1] As the progeny trees were 2 and 3 years old when planted on the plots, the total ages represented by these measurements are 22 and 23 years.

Average diameters at breast height (4.5 feet above ground) 20 years after outplanting were read from height-diameter curves made for all plots (table 10). They ranged from 3.0 inches for the Lolo progeny to 1.2 inches for the Santa Fe and Ashley progenies. Table 11 presents average heights and diameters of dominant trees.

TABLE 10.—*Diameter of progeny trees after 20 years' growth on plots* [1]

Region, locality, and altitude (feet) of seed origin	Average	Standard deviation	Standard error	Basis, trees
	Inches	*Inches*	*Inches*	*Number*
North Pacific: Siskiyou (2,000)	2.8	±1.5	±0.32	21
North plateau:				
Boise (5,500)	2.1	±1.4	±.17	68
Payette (5,000)	2.0	±1.3	±.19	44
Whitman (5,000)	1.8	±1.3	±.23	30
Umatilla (3,500)	2.2	±1.5	±.25	36
Colville (2,700)	2.4	±1.4	±.16	85
Kaniksu (2,600)	2.6	±1.2	±.15	58
Lolo (3,000)	3.0	±1.3	±.15	81
Bitterroot:				
4,000	2.9	±1.1	±.22	65
5,000	2.5	±1.2	±.13	85
7,200	2.3	±1.1	±.19	35
East of Continental Divide:				
Helena (4,500)	2.0	±1.2	±.13	87
Custer (3,200)	1.4	±1.1	±.13	70
Harney (5,000)	2.0	±.7	±.08	78
Roosevelt (8,000)	1.5	±1.3	±.24	27
San Isabel (8,000)	1.7	±1.2	±.21	36
South plateau:				
Coconino (7,100)	1.8	±1.2	±.15	63
Santa Fe (8,000)	1.2	±1.0	±.02	16
Central plateau: Ashley (7,500)	1.2	±.9	±.01	43

[1] See footnote 1, table 9.

TABLE 11.—*Average height and diameter of dominants among progeny trees after 20 years' growth on plots* [1]

Region, locality, and altitude (feet) of seed origin	Height	Diameter	Basis, trees	Region, locality, and altitude (feet) of seed origin	Height	Diameter	Basis, trees
North Pacific: Siskiyou (2,000)	*Feet* 17.3	*Inches* 4.5	*Number* 7	East of Continental Divide:	*Feet*	*Inches*	*Number*
North plateau:				Helena (4,500)	16.6	3.1	28
Boise (5,500)	17.2	4.2	13	Custer (3,200)	13.6	2.4	9
Payette (5,000)	13.8	3.1	11	Harney (5,000)	13.8	2.9	23
Whitman (5,000)	15.0	3.8	6	Roosevelt (8,000)	12.3	2.8	6
Umatilla (3,500)	15.3	3.4	11	San Isabel (8,000)	13.2	3.1	7
Colville (2,700)	17.4	4.2	26	South plateau:			
Kaniksu (2,600)	16.5	3.9	20	Coconino (7,100)	12.8	3.2	13
Lolo (3,000)	21.3	4.6	24	Santa Fe (8,000)	9.7	2.2	6
Bitterroot:				Central plateau: Ashley (7,500)	10.9	2.5	8
4,000	18.3	4.0	23				
5,000	17.3	3.7	22				
7,200	17.2	3.9	10				

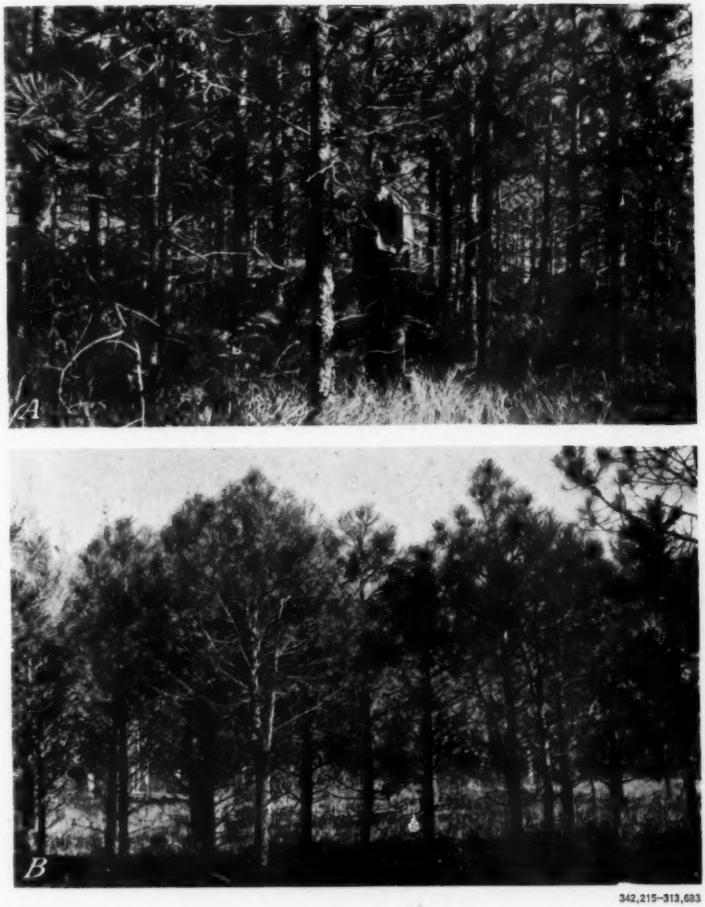
[1] See footnote 1, table 9.

TABLE 12.—*Regional averages of height and diameter of progeny trees after 20 years' growth on plots* [1]

Region or locality of seed origin	Average height [2]	Range of plot heights	Average diameter [2]	Basis, plots	Region or locality of seed origin	Average height [2]	Range of plot heights	Average diameter [2]	Basis, plots
	Feet	*Feet*	*Inches*	*Number*		*Feet*	*Feet*	*Inches*	*Number*
North Pacific	11.9	.....	2.8	1	East of Continental Divide	10.0	8.6–11.1	1.7	4
North plateau	12.5	9.4–15.7	2.4	10	South plateau	8.6	7.5–9.0	1.7	2
Helena	12.8	.....	2.0	1	Central plateau	7.2	.....	1.2	1

[1] See footnote 1, table 9.
[2] Regional values shown are weighted averages of locality averages.

In table 12 a comparison is made among the regions as to average heights and diameters of progeny. Statistical analysis by the method of variance shows no significant differences in average height



342,215–313,683

Stand views of progeny plots in 1935: *A*, Straight, tall, well-formed stems of Lolo progeny; *B*, slightly crooked and rapid-tapering stems, open branches, and rounded slow-growing tops of Coconino progeny.

270,758

General view of Bitterroot 5,000 plot in 1932, showing tree form and pointed crowns typical of north plateau progenies.

between North Pacific progeny (1 plot), north plateau progenies (10 plots), and Helena progeny (1 plot). On the other hand, the difference in average height between progenies derived from localities east of the Continental Divide (4 plots) and north plateau progenies is statistically significant, and so are the differences between south and north plateau progenies and central and north plateau progenies. Thus it is shown that the progenies derived from the south and central plateaus and the region east of the Continental Divide are truly of slow growth in northern Idaho.

RELATION OF HEIGHT TO DIAMETER

Another growth characteristic of interest to the forester is the height-diameter relation, which reflects capacity to make volume and quality growth. In the absence of data for the determination of form factors, height as related to diameter at breast height was taken from the curve made for each plot. The data are presented in figure 4.

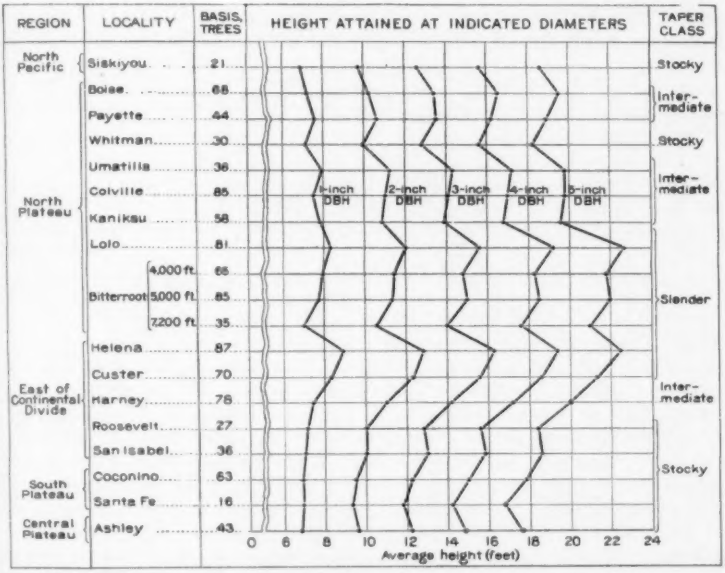


FIGURE 4.—Relation of average height of progenies to diameter in the various plots. (Dots indicate actual and circles interpolated data.)

Great differences in form are evident. For example, average height of trees 5 inches in diameter is 22.7 feet on the Lolo plot but only 16.8 feet on the Santa Fe plot. The range of differences was divided into three equal parts representing the three taper classes slender, stocky, and intermediate, of which slender is the most desirable and stocky the least desirable. Progenies in the slender class are the Lolo, Helena, Custer, and Bitterroot; those in the stocky class are the Santa Fe, Ashley, Coconino, Roosevelt, San Isabel, Whitman, and Siskiyou. Plate 5 presents examples of progenies having (*A*) well-formed stems and (*B*) poorly formed stems. Plate 6 shows the general form and

pointed crowns of a typical north plateau progeny. (Compare with pls. 4, *C*, and 5, *B*, illustrating the characteristic rounded crowns of typical south plateau progenies.) Attention is again called to the wide spacing of the surviving trees of the Siskiyou and Santa Fe progenies; it is not known what differences their stem forms would show if they had developed in closed stands.

It is believed that the data for ages 22 to 25 years represent the height-diameter ratios of most of the trees from youth to maturity. Because of comparatively early falling off of height growth in the Custer and Harney parent localities, however, it is reasonable to assume that the stem form of the two progenies will deteriorate later in life. On the other hand, the Whitman and Siskiyou progenies may be expected to continue height growth longer and improve in stem form, like the trees in their parent localities.

RELATIVE HEIGHT GROWTH BY YEARS

In studying introduced species and races, foresters both in Europe and in the United States have been inclined to judge the relative growth possibilities of different progenies from their behavior during

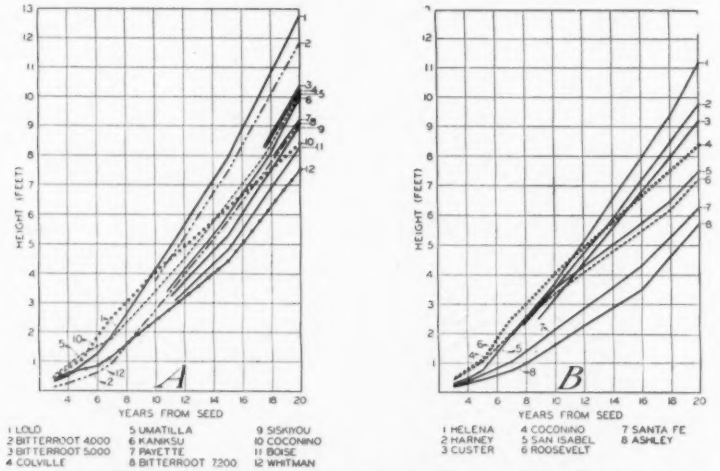


FIGURE 5.—Relative height growth, by year, of progenies derived (*A*) from North Pacific and north plateau sources, and Coconino; and (*B*) from south and central plateau and east of Continental Divide. Sources are indicated by number.

the first few years. This has not always been justified by the character of growth made in later years. Some introduced races that have made strikingly rapid height growth in the first few years have later fallen behind local races. The height measurements taken annually from 1912 to 1919 and those taken in 1927 and 1935 have made it possible to plot curves that show effectively the trends of early height growth in this experiment.

The height curves of the north plateau and North Pacific progenies and the Coconino progeny, given in figure 5, *A*, show that the Coconino progeny grew faster than any of the others during the first 10

years. Gradually, however, its growth rate has become less rapid, and local races have been overtaking it. The Lolo progeny, which in 1935 was growing more rapidly than any other, passed it at 10 years, the Bitterroot 4,000 at 11 years, the Umatilla at 14 years, and most of the others by 18 years.

Figure 5, *B*, shows that the Coconino progeny was foremost in height growth among the progenies derived from the central and south plateaus and from east of the Continental Divide, until the Helena, Harney, and Custer progenies overtook it between 11 and 15 years. The Roosevelt, San Isabel, and Umatilla progenies also excelled in height growth at the start but were soon overtaken by local progenies.

This comparison is evidence that initial growth rate of introduced races should not be accepted as presaging the later development of the trees. The trends shown here may, indeed, be taken as a warning not to apply too far into the future the present conclusions from results at 22 to 26 years of age.

GROWTH OF PROGENIES COMPARED WITH GROWTH IN PARENT LOCALITIES

If an experiment such as that described here shows, for example, that a given introduced race is much slower in growth than a local race, and therefore unsuitable for planting as a timber crop, this indication ordinarily meets the needs of the practicing forester. The findings are much more valuable, however, if they indicate further whether the growth rate of the introduced race is hereditary or is due to a difference in environment. As one of the purposes of this experiment is to determine what characteristics are heritable, an effort has been made to ascertain the growth rates of ponderosa pine in the parent localities.

Suitable growth data have been made available for the general localities of seed origin through a recent interregional yield study [7] of even-aged ponderosa pine stands in the northern part of the range of the species, from the Black Hills to California. The data used in this yield study included average heights of dominant and codominant trees by decades for each of 13 site classes. From these data and from measurements yielding average site indices made in the general localities of seed origin, it was possible to plot the curves for this portion of the range shown in figure 6, *A*. As the basic data were intended solely for use in constructing yield tables, they were deficient in measurements of stands less than 25 years old. Therefore the lower portions of the curves had to be constructed by extension, and the heights indicated are close approximations only. These curves are sufficiently accurate, however, to serve in comparing rates of growth in the different localities. The curve shown in figure 6, *A*, for Arizona and New Mexico (south plateau) was plotted from growth measurements made by H. M. Curran, in his report already cited. Data on rates of growth are not available for the specific localities of seed origin in Utah, Colorado, or western Oregon.

To construct figure 6, *B*, average heights of dominant and codominant progeny trees at 20 years were plotted and a straight line was drawn from each plotted height to the origin point.

[7] This study was supervised by W. H. Meyer, then of the Pacific Northwest Forest and Range Experiment Station, and the site-index data here used were supplied by him. The contribution to this study from the Northern Rocky Mountain Region consisted of data on 101 yield plots in northern Idaho, 99 in western Montana, and 35 in eastern Montana.

In studying figure 6 it will be seen that the curves representing the western Montana, northern Idaho, and southern Idaho stocks occupy the upper part of the growth range both of native trees and of progeny trees, and that the curves for eastern Montana, Black Hills, and south plateau stocks occupy the lower part of each range. The curve for the Arizona and New Mexico trees is lower than all the others in *A*, and conspicuously so in *B*.

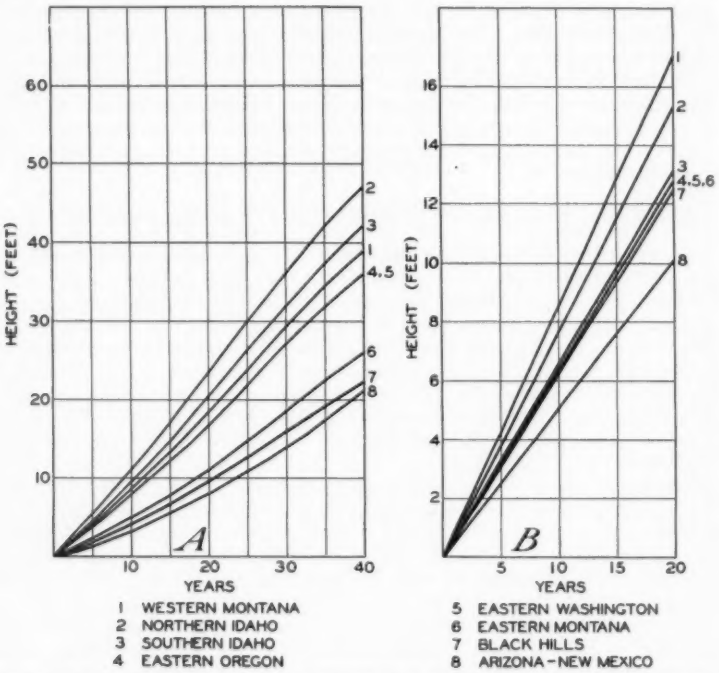


FIGURE 6.—Average heights of dominant and codominant trees (*A*) of some of the parent localities and (*B*) of some of the progeny plots. Seed sources are indicated by number.

It appears that progenies from localities of more severe climate than northern Idaho have inherited the slow growth rates typical of such localities. This agrees with findings of numerous European investigations (*5*, *6*, *8*, *12*, *18*, *35*). As shown by the present study, the inheritance is strongly maintained through more than 20 years of the first generation. More extended experiments in Europe described by Dengler (*9*) and Münch (*21*) indicate that inherited growth characteristics are maintained also in trees of the second generation of introduced races.

In the single case (Siskiyou) of a progeny originating in a climate considerably milder than that of the experimental site in northern Idaho, the rapid growth rate of trees in the region of origin was not exhibited by the progeny. The site indices for the northern Sierra

territory, embracing the Siskiyou and Shasta seed-source localities (not included in fig. 6), are much higher than those for any other part of the range of ponderosa pine included in this study. The Siskiyou progeny trees surviving the severe winter freeze in 1924 that killed all the Shasta progeny have grown fast, but not so fast as trees in the parent locality. This indicates the inhibiting influence of climatic conditions more severe than those of the parent habitat. Büsgen and Münch (*6*), Dengler (*9*), and others have pointed out similar results of introducing races from a mild climate to a cold one. There is here, of course, no indication that progeny of the same Siskiyou parent trees would fail to inherit rapid growth rate if planted in localities of mild climate. Rate of growth is a quantitative characteristic that is modified by environment as well as by inheritance.

PHENOLOGICAL CHARACTERISTICS

Among the factors that have an important bearing on the adaptability of progeny to a given climate, in addition to needle structure, are the parent trees' characteristics as to time of beginning and ending seasonal growth. In this connection Büsgen and Münch (*6*) state:

> Races of trees from regions with a short growing season and bad forest growth, when transplanted to mild situations, retain the short duration of their vegetation, fail to utilize the longer growing season, and so remain behind the indigenous local races. In general they come into leaf earlier, it is true, because less heat suffices for their vegetation, but they cease their growth early in the summer. When the transfer is in the opposite direction the trees seek to retain their inherited long vegetative period, grow on into the autumn and perish with frost.

That vigor of growth and susceptibility to disease as well as to frost are in large measure determined by inherited phenological habits has been shown by many investigators (*5*, *8*, *9*, *12*, *18*, *19*, *20*, *34*).

Phenological observations have not been made on the progeny plots, but have been conducted for 8 years on native conifers near the experimental site. They show that the date when the buds on indigenous ponderosa pine begin to burst ranges from April 12 to May 25, averaging April 29. In the Coconino parent locality, Pearson (*25*) observed during a period of 3 years that buds of ponderosa pine begin to burst from May 15 to May 25. Thus the growing season of the Coconino locality begins about 3 weeks later than that of the Kaniksu locality. The fact that the Coconino progeny has a short period of vegetative activity presumably has been one cause of the comparatively small growth it has attained at 20 years (fig. 5, *B*). On the other hand presumably the long period of growth activity characteristic of trees in the North Pacific region, transmitted to the Siskiyou progeny, has been one of the causes of the frost damage suffered by the latter in northern Idaho.

GEOGRAPHIC RACES INDICATED

The data on foliage and growth characteristics obtained in this study, together with information on climate in different parts of the range of ponderosa pine, clearly point to the existence of several forms or races. The grouping of localities of seed origin by similar foliage characteristics and the discussion in that connection have already indicated general racial trends. It remains to present

evidence contributed by an examination of climate and growth characteristics. Fine distinctions are not attempted. It is realized that in addition to the characteristics studied, racial distinctions depend also upon differences in cones,[8] bark, and wood, disease resistance, and other factors not dealt with in this study. The data most indicative of racial differences are shown in tables 8 and 12. In this connection, attention is directed also to figures 1 and 2 and to tables 1 and 2.

NORTH PACIFIC REGION

Trees of the North Pacific region differ from those of the remainder of the ponderosa pine range chiefly in that they are adapted to a mild, equable climate and are poorly equipped to withstand low temperatures. Their leaf structure is distinct from that of the trees of any other region studied, since very few of the hypoderm cells have thick walls. In this region extremely low temperatures are unknown, and the frostless season is longer and total precipitation much greater than in any of the other ponderosa pine regions studied. The fact that all the progeny trees derived from one of the two seed-source localities in this region and most of those from the other died as a result of the precipitous drop in temperature on December 15, 1924, from 45° F. to −12° F. in 20 hours, may be traced to the absence of protective hypodermal thickening. Both rainfall and precipitation effectiveness are high in the North Pacific region, and growth is consequently better there than in any of the other regions. The evidence seems to indicate that the ponderosa pine of the North Pacific region is a race by itself.

NORTH PLATEAU REGION

The foliage of the north plateau trees resembles that of the North Pacific trees in length, slenderness, and flexibility of needles and in occurrence of three-needle fascicles, but it has a distinct moderate hypodermal thickening, which presumably has a part in enabling the trees to resist severe low temperatures better than those of the North Pacific region. The progenies derived from this region suffered little loss from the freeze of December 15, 1924. Growing-season precipitation and temperature are favorable and growth in the parent localities is better than in any of the other regions studied except the North Pacific. The growth of many of the progenies greatly excelled that of progenies from other regions. On the basis of structural adaptation to low temperatures, the north plateau trees constitute a race distinct from the North Pacific trees.

REGION EAST OF CONTINENTAL DIVIDE

As already brought out, the external foliage characteristics of progeny and native trees of the region east of the Continental Divide differ conspicuously from all others in this experiment except those of the Ashley locality in Utah. The outstanding characteristics of the foliage of ponderosa pine in this region are the prevailing occurrence

[8] Until 1936, cones were borne by the progeny trees only singly and sporadically. Counts in 1936 showed that 11 percent of the Helena trees bore 84 cones; 7 percent of the Roosevelt trees, 24 cones; 3 percent of the Umatilla trees, 9 cones; 2 percent of the Payette, 15 cones; 2 percent of the Kaniksu, 12 cones; and 2 percent of the Lolo, 3 cones.

of two-needle fascicles, the shortness, thickness, and stiffness of the needles and their compact arrangement on the branches, and the large number of rows of cells and heavy thickening of the cell walls in the hypoderm. Rate of growth is mostly slow. The progenies derived from this region have displayed a high degree of hardiness (*14*). Altogether these distinctive characteristics make this a strongly demarcated race.

SOUTH PLATEAU REGION

In moderate length and slenderness of needles and in percentage of three-needle fascicles, the trees of the south plateau show relationship to those of the north plateau and North Pacific regions. The southern form, however, is distinctly different in its conspicuously heavy thickening of hypoderm cells, slightly stiff rather than flexible needles, and much slower rate of growth. The south plateau trees differ also from the trees typical of the region east of the Continental Divide, although internal leaf structure is the same in both forms. Existence of a distinct south plateau race is strongly evident.

CENTRAL PLATEAU REGION

The Ashley locality of seed origin, lying well within the central plateau region, has a lower annual precipitation than any of the other localities of the study, a pronounced deficiency of spring precipitation, and a generally low availability of moisture throughout the growing season. Its annual and summer averages of temperature are among the lowest. Thus precipitation and temperature together form a climate very rigorous for tree growth. This is reflected in the fact that the growth of the Ashley progeny, both in height and in diameter, was less than the average for any regional group of progenies. The needles are short, thick, and stiff and compactly arranged on the branches, as in the region east of the Continental Divide. Number of rows of hypoderm cells and thickness of the cell walls are the greatest found in this study. Foliage occurs mostly in fascicles of three, but many trees contain up to 40 percent of two-needle fascicles.

Thus the trees of this locality have a strong relationship to the trees east of the Continental Divide and have relatively little in common with those of the south plateau. In view of this, the Ashley trees are regarded as of the same race as those east of the Divide.

As indicated by Korstian (*16*) and by Baker and Korstian (*2*), the Ashley form of tree is found over much of Utah, Nevada, and the remaining territory included in the central plateau.

HELENA LOCALITY

In the Helena locality, 15 to 20 miles east of the Continental Divide, the foliage is strongly three-needled, with needles of medium length and moderate hypoderm thickening, thus resembling that of the north plateau more closely than that of localities farther east. The height growth of the Helena progeny, moreover, is as great as the average for north plateau trees and outstandingly better than that of other progenies derived from east of the Divide. Altogether, the evidence indicates so close a relationship that the Helena trees may be regarded as belonging to the north plateau race.

RACES SUMMARIZED

Briefly, the races tentatively indicated in this study and their important earmarks are the following:

1. *North Pacific race.*—Typically three-needled, needles long, very little thickening of hypoderm, rapid growth, relatively low frost resistance.
2. *North plateau race.*—Typically three-needled, needles long, distinct moderate thickening of hypoderm, good growth, good frost resistance.
3. *South plateau race.*—Typically three-needled, needles medium to long, very thick hypoderm structure, growth slow, good frost resistance.
4. *Race found east of Continental Divide and on the central plateau.*—Typically two-needled, needles short, very thick hypoderm structure, growth slow, highly frost-resistant.

Study of foliage from trees at Quincy, Calif., in the South Pacific region (no progeny available) shows fascicles very typically containing three needles. Needles are long and contain moderately thickened hypoderm. The data reveal a very close relationship to the North Pacific and north plateau trees, but are not adequate for ascertaining racial distinctions.

SUITABILITY OF RACES FOR PLANTING IN NORTHERN IDAHO

Decision as to the desirability of a tree race for introduction in a new locality involves consideration of both its adaptability to the local climate and its suitability for timber production. No matter how hardy and disease-resistant a race may be in the new locality, it will be useless for timber-crop production if it grows too slowly and develops a poor, stunted form.

Adaptability to climate unfortunately can be judged only by actual performance; and it has been learned by experience elsewhere that such performance, to be clearly indicative, must extend over at least one-third of the tree's life to maturity. The history of introduced races is replete with instances of break-downs of stands 25 to 40 years after planting. In the classic example described by Wibeck (*34*), many thousand acres of Scotch pine plantations in Sweden, derived from unsuitable seed sources, died out or developed poor form after having thrived well for 25 or more years. Similar happenings elsewhere in Europe have been reported by numerous writers (*3*, *7*, *9*, *11*, *13*). In South Africa, where the maritime pine (*Pinus pinaster*) of the Mediterranean countries proved to be an excellent species for introduction, Duff (*10*) shows that more than 285,000 pounds of maritime pine seed were imported between 1898 and 1914 with little or no regard for seed origin. Although many of the plantations have thrived and developed into stands of excellent growth rate and form, others, established with seed from unsuitable sources, at 40 years of age are of slow growth and stunted form or badly infected with disease. In the United States, although forest planting on an extensive scale is not so old, some plantations of introduced species that had an auspicious beginning have already broken down. These include several Scotch pine plantations in Pennsylvania [9] that made exceedingly rapid, straight, and vigorous growth and gave high promise of being hardy

[9] AUGHANBAUGH, J. E. SCOTCH PINE—AN ENIGMA. Pa. Dept. Forests and Waters Serv. Letter. 1935.

and adaptable until they were 20 to 25 years old, but then began to disintegrate badly through inability to withstand adverse conditions as to wind, snow, insects, and disease.

Thus it would be premature to make a statement on the ultimate adaptability to northern Idaho and adjacent territory of the progenies introduced in this experiment. Certain present indications of relative adaptability may be pointed out, however, with the warning that some future combination of climatic conditions may upset them.

The chief factors in climatic adaptability and suitability for timber growing are frost hardiness, disease resistance, rate of growth, and form. So far the progenies at the northern Idaho experimental site have not been seriously infected with disease and have developed only slight defects in stem form. They have, however, shown marked differences in growth rate and in relative resistance to untimely freezing temperatures.

It is well to keep in mind in this connection that individual parent trees may vary considerably in their ability to produce good or poor progeny in these respects. Although such differences between individual parents may account for some of the variation among trees of a given progeny plot in this experiment, it is believed that the plot averages are fairly safe to use in comparing the relative growth capacity and climatic adaptability of progenies derived from different localities.

The Siskiyou and Shasta stocks, which make rapid growth but are poorly equipped to resist frost, should not be considered for use in northern Idaho; and on the basis of extremely slow growth the Ashley, Roosevelt, San Isabel, Santa Fe, and Coconino stocks, with progeny heights averaging only 7.2 to 9.0 feet at 20 years, should also be excluded, despite the great hardiness of most of them. All the progenies other than those derived from the North Pacific region have withstood the severe freezes in northern Idaho during the period covered by this experiment, apparently because of their marked protective thickening of the hypoderm.[10]

According to the evidence obtained in this study, a progeny derived from a cold climate and grown in a milder climate exhibits slow growth and immunity to frost; a progeny derived from a mild climate and grown in a colder climate has low frost resistance and fails to exhibit the parental characteristic of rapid growth. Progenies introduced into the North Pacific region from any other part of the range of ponderosa pine would thus be expected to grow more slowly than native trees; and in the central and south plateaus and east of the Continental Divide, progenies introduced from the Pacific coast and the north plateau probably would suffer heavy losses by freezing and would grow more slowly than trees in their parent localities.

Such evidence as is available from similar experiments seems to confirm this reasoning. Near Carson, Wash., in the North Pacific region, in a 14-year-old experiment with ponderosa pine progeny,[11] offspring derived from the Bitterroot National Forest, Mont., grew very well but less rapidly than the local races, while progenies of Arizona, New Mexico, and Black Hills origin made the least height growth, as in the northern Idaho experiment. Near Manitou, Colo., in

[10] Evidence of the effect of inherited hypodermal protection, in addition to that afforded by the freeze of December 1924, is the fact that trees in Savenac Nursery, in western Montana, grown from Custer seed, survived an October 1935 freeze with almost no sign of damage, whereas local stocks suffered some damage.

[11] Data supplied by the Pacific Northwest Forest and Range Experiment Station.

a 15-year-old experiment with ponderosa pine progenies,[12] the trees of local Roosevelt and San Isabel origin were hardiest and tallest, while those grown from seed derived from the Bitterroot (Mont.) and Tusayan (Ariz.) National Forests were shortest and most subject to losses. Only 5 and 12 percent, respectively, of the latter survived, and their height was only one-third that of the local progenies. Pearson (*25*) reported that first-year seedlings of ponderosa pine grown in a nursery near Flagstaff, Ariz., from seed collected on the Sierra National Forest, Calif., were completely killed by a November freeze, whereas those grown from seed collected in Arizona, New Mexico, Colorado, and the Black Hills were not injured. In an unpublished report he stated that ponderosa pine progenies grown near Flagstaff from seed collected in various localities in the northern part of the range of the species all died within 5 or 6 years.

Elimination of the Ashley, Roosevelt, San Isabel, Santa Fe, Coconino, Siskiyou, and Shasta progenies as unsuitable for introduction in northern Idaho leaves 13 progenies, showing excellent to fair growth and having hardiness also in their favor, that must be given consideration as to suitability from a timber-growing standpoint. Ten of these are from localities in the north plateau region and three from localities east of the Continental Divide. Those making rapid height growth are, in order, the Lolo, Bitterroot 4,000, Bitterroot 5,000, Helena, Kaniksu, Colville, Umatilla, and Bitterroot 7,200. The Lolo and Bitterroot 4,000 progenies have a distinct lead over all others in height. The differences among the heights attained by the six other leading progenies are probably not significant, and for the present purpose all six may be regarded as equal in growth capacity. The slower growing of the north plateau progenies thus far are the Payette, Boise, and Whitman.

The Custer and Harney offspring are comparable in rate of growth with the slower growing of the north plateau progenies. As has already been pointed out, in the native localities of these two progenies the height growth of ponderosa pine falls off earlier than in the north plateau region; it is reasonably safe to assume, therefore, that in northern Idaho these progenies will fall far short of the ultimate height growth of trees of local origin. A strong point in their favor is high resistance to sudden drops in temperature below the freezing point (*14*). It is doubtful, however, whether this advantage can, even in the long run, compensate the faster growth of such local progenies as the Lolo, Bitterroot, Colville, and Kaniksu.

The Helena progeny shows not only a high degree of frost resistance but also a good rate of growth, comparable to those of the Kaniksu and Colville progenies. This indicates the Helena locality as a safe source of seed for planting in northern Idaho when local cone crops are inadequate.

Why the introduced Lolo and Bitterroot 4,000 progenies so definitely surpass the local Kaniksu stock in both growth and hardiness is difficult to explain on the basis of the data now available. Rainfall and temperature records and soil-moisture tests shed but little light on the subject; and as has already been indicated, leaf structure is about the same for all three of these progenies. Perhaps the better part of wisdom would be to keep in mind the example of the rise and fall in height supremacy of the Coconino progeny, shown in figure 5,

[12] Data supplied by the Rocky Mountain Forest and Range Experiment Station.

and not attempt finely drawn explanations of the relative order of these north plateau progenies, on the basis of climatic or any other records.

It would appear that the most suitable general territory in which to collect seed for planting in northern Idaho (and western Montana) extends roughly from the Colville locality, in Washington, to a little beyond the Continental Divide, and from the latitude of the Salmon River approximately to the Canadian boundary.

SUMMARY AND CONCLUSIONS

Trees grown from seed of ponderosa pine collected in 20 localities in the western United States, widely separated geographically or in elevation, were planted on the Kaniksu National Forest, in northern Idaho, in the years 1911–17. Location and climate of the seed sources were known, but no data were recorded as to their soils or the individual characters of parent trees. Measurements of progeny trees were made in each of the years 1912–19, in 1927, and in 1935. At the time of the 1935 measurement the trees were 22 to 26 years old from seed.

A study of external and internal foliage characteristics of the progenies was made as a part of the 1935 examination of the plots. Differences in respect to number of needles to the fascicle, length of needles, general appearance of foliage, and thickening of hypoderm were found among progeny groups derived from five different regions within the range of ponderosa pine in the United States, which were delimited on the basis of precipitation type. These regions were designated North Pacific, north plateau, central plateau, south plateau, and east of the Continental Divide; the sixth region, the South Pacific, was not represented by any of the seed used.

Differences among the progenies in number of needles to the fascicle, length of needles, general appearance of foliage, and rate of growth corresponded to differences among the trees of the parent localities. The conclusion is drawn that these characteristics are strongly heritable in ponderosa pine and will appear in the offspring in any new environment where the trees will grow, at least for more than 20 years of the first generation.

Pronounced differences were exhibited by the different progenies in height and diameter growth. The slowest-growing progenies made only half as much growth as the fastest-growing. The best growth in height and diameter was made by trees derived from localities in the north plateau region resembling the locality of the planting site in climate. The poorest growth was made by trees derived from localities in Colorado, Utah, Arizona, and New Mexico that have more severe climates. Hereditary growth tendencies were less marked in the one progeny derived from a region having a climate considerably milder than that of the experimental area.

Characteristics as to persistence of needles were found not to be hereditary.

A study conducted cooperatively with the University of Montana revealed strong evidence that characteristics of internal structure of needles were inherited.

The present findings, revealing the existence of racial strains in ponderosa pine varying in rate of growth and hardiness, indicate that a tree's growth rate and hardiness should be investigated critically and the climatic characteristics of the locality in which it is

growing compared with those of the proposed planting site before the seed is used for reforestation. They indicate tentatively that the most suitable general territory in which to collect ponderosa pine seed for planting in northern Idaho is that extending from the Colville locality, in Washington, eastward a little beyond the Continental Divide and from the Salmon River to the Canadian boundary.

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THE ROLE OF INSECTS IN THE DISSEMINATION OF POTATO BLACKLEG AND SEED-PIECE DECAY[1]

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INTRODUCTION

The important role of insects as vectors of plant diseases is one of the most striking developments in the field of phytopathology. This paper reports a study of the part taken by certain insects in the dissemination of blackleg (*Bacillus phytophthorus* Appel) and seed-piece decay in the potato (*Solanum tuberosum* L.), also some of the factors that influence the attack by insects and the consequent development of these diseases.

According to Leach (*12, p. 150*),[3] "von Hegyi [in 1910], working in Polish Galicia and Prussian Silesia, found such a close correlation between blackleg and wire worm attack that he held biting insects to be a necessary factor for entry of the parasite." Jennison (*7*), who studied the problem in the United States, found the larvae of insects in and on the affected tissues but stated that there was no positive evidence that they were active agents in the dispersal of the disease.

Leach (*11, 12*) showed that the seed-corn maggot (*Hylemyia cilicrura* Rond.) has an active part in the spread and development of potato blackleg. Bonde (*1*) by means of controlled laboratory experiments confirmed Leach's conclusion. In later work Bonde, and also Reid et al. (*17*), showed that the penetration of the seed-corn maggot into potato seed pieces is often dependent on small, primary, bacterial lesions formed in the cut surfaces. Bonde (*2*) reported that the closely related seed-potato maggot, *H.* (*Phorbia*) *trichodactyla* Rond., may also transmit the disease.

Leach (*13*) found that two insects (*Scaptomyza graminum* and *Elachiptera costata*) are common agents of inoculation of celery heart rot. This disease is caused by *Erwinia carotovora* (Jones) S. A. B., the cause of blackleg and seed-piece decay in the potato. Johnson (*9*) and Bonde (*3*) demonstrated that the cabbage maggot (*Hylemyia brassicae* Bouche) may transmit a similar soft rot to members of the Cruciferae. The fact that several insects had been reported as being vectors of the soft-rot organisms led to further studies of the relation of insects to potato seed-piece decay and blackleg.

STUDIES WITH THE ANTHOMYIIDS

According to Leach (*12*) a symbiotic relationship exists between the pathogenic organism of blackleg and the seed-corn maggot, one of the anthomyiids. The eggs while being deposited in the soil may become contaminated by pathogenic bacteria, and the young maggots

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[3] Italic numbers in parentheses refer to Literature Cited, p. 916.

may introduce this inoculum into the planted potato seed pieces. These pathogens and other microorganisms are present in the internal portion of the pupal and larval stages as well as on the surface of the eggs (*15*, *16*).

HABITS AND LIFE HISTORY OF THE SEED-CORN MAGGOT (HYLEMYIA CILICRURA ROND.)

The seed-corn maggot is widely distributed in both Europe and the United States (*5*, *pp. 949–976*). The literature on the economic losses caused by this insect is extensive. It shows that probably the larvae of this insect will attack practically any of the succulent and tender vegetable crop plants as well as grain, grasses, and weeds, provided conditions are favorable.

The life cycle of the seed-corn maggot under Maine conditions is not entirely known. In northeastern Maine the adults generally become prevalent in the spring at potato-planting time, especially after a few warm days. In 1932 flies from the overwintering puparia were emerging from the soil in great numbers on May 17, 18, and 19, following several days of warm weather. These flies, which are most abundant from the middle of May until the middle of June, appear to be attracted to the moist and freshly turned soil and are especially active following a warm rain. They soon commence to deposit eggs in the soil. Within a few days the eggs hatch, and the small larvae begin to feed on nearby vegetable matter. Under the conditions in Aroostook County the larvae are full grown within from 7 to 12 days, at which time they leave the vegetable substratum, enter the nearby soil, and pupate. On June 16, 1932, maggots that were full grown and about to pupate were found in decayed seed pieces. The adult insects from the overwintering puparia had practically disappeared by June 21, and the second brood was emerging. These also disappeared within 1 or 2 weeks.

The adult as well as the other stages may be noted to some extent during the entire summer. However, during July and early August the number of adults greatly diminishes; but usually they become quite numerous again the latter part of August and in September, and larvae have been found in decaying potato tubers affected with late blight. Potato tubers affected with late blight rot, followed by bacterial organisms, serve as a favorable host for *Hylemyia cilicrura* in late summer in northern Maine.

Puparia have been seen in the latter part of September and in early October. These late puparia apparently overwinter in the soil. The writer has overwintered puparia in soil in the field and reared them to adults the following spring.

The writer has not been able to demonstrate that the adult flies are attracted to decaying potato tubers and foliage. He has exposed healthy and decayed seed pieces to fly infestation in the field. Flies, although numerous, were not attracted more by the rotted tubers than by healthy ones.

In order to test the preference of the flies toward potato material, freshly cut seed pieces and uncut tubers were alternated in the field and exposed to flies under natural conditions. Notes were taken of the number of flies that visited the 2 lots of seed in 10-minute periods. An average of 62 anthomyiids visited the surfaces of the freshly cut

seed, and only 10 visited the uncut tubers. The flies apparently were attracted by the moisture and possibly by the odor of the freshly cut tubers. The flies are also attracted to fish and cottonseed meal when used as bait in insect traps exposed in the field.

During the egg-laying period the female flies are seen about potato seed pieces, clods, stones, or organic debris lying on the plowed fields, apparently in search of sheltered nooks or crevices for depositing their eggs. The female pushes the surface soil away with her hind legs, inserts her extensile ovipositor into the moist soil, and deposits the small, white, crescent-shaped eggs just beneath the surface sometimes on or near the planted potato seed pieces. Figure 1 shows eggs that

FIGURE 1.—Eggs of the seed-corn maggot that were deposited in the soil in a field. Approximately ×15.

were deposited in the soil in a field. From several to a dozen or more may be deposited at a place.

SEED-POTATO MAGGOT (HYLEMYIA TRICHODACTYLA ROND.)

Johannsen (*8*) found the seed-potato maggot (*Hylemyia trichodactyla* Rond.) infecting a lot of seed potatoes from Aroostook County. He states that as this insect has a wide distribution and is fairly common, it is not unlikely that it is of economic importance. The writer has reared this insect from rotted potato seed pieces obtained from the field and has caught the adults by sweeping with a net and by using baited traps.

Although the seed-potato maggot possibly has a wide range of hosts, the writer has obtained it only from decaying potato material

and has caught it only in potato fields. The seed-corn maggot, on the other hand, has been secured in Aroostook County not only from potatoes, but also from seedlings of corn, beans, peas, and cucumbers. The data at hand would suggest that *Hylemyia trichodactyla* has a more specific preference for potato tissue than has *H. cilicrura*.

Examination of the flies caught with an insect net, or with baited traps, suggests that the seed-potato maggot is more prevalent in Aroostook County than the seed-corn maggot, especially in the vicinity of potato fields. Studies also indicate that the life history of these two insects is essentially the same.

ASSOCIATION OF PATHOGENIC BACTERIA WITH DIFFERENT STAGES OF THE SEED-CORN MAGGOT

Leach (*12*) found that pathogenic bacteria could be isolated from the different stages in the life cycle of the seed-corn maggot. He (*16, p. 160–161*) also demonstrated that the bacteria "survive in the lumen of the midintestine, in the cast-out linings of the fore- and hind-intestine, and in the space between the prepupal cuticle and the true pupa."

Although the writer has made no attempts to determine the exact place where the bacteria are harbored within the insect, he has made isolations from the different stages, which confirm Leach's results.

Leach showed that the surface of the egg may become contaminated in the process of oviposition. In 1929 the present writer secured only 1 pathogenic organism from the surface of eggs in 16 attempts, while in 1930 he secured 3 in 10 attempts (table 1). The adults were induced to deposit their eggs in pans of sterilized soil in the laboratory, and the eggs were removed with a moistened sterile needle to tubes of beef broth. The cultures were incubated until bacterial development was apparent and then tested for pathogenicity on potato slices.

TABLE 1.—*Isolation of pathogenic bacteria from the different stages in the life cycle of the seed-corn maggot, Presque Isle, Maine* [1]

Year	Lot No.	Stage of insect	Source of insect	Total	Pathogenic		Types of decay
				Number	*Number*	*Percent*	
1927	1	Pupa	Laboratory [2]	5	1	20	White.
1929	1	Egg	Deposited in sterile soil	16	1	6	White, rapid.
	2	Adult	Captured in field	28	2	7	Dark.
	3	Pupa	Decayed pea seed	32	7	22	White, rapid.
	4	do	Laboratory [2]	38	16	42	Do.
1930	1	Egg	Deposited in sterile soil	10	3	30	Do.
	2	Adult	Captured in field	14	1	7	Dark.
	3	do	do	20	2	10	Do.
	4	Pupa	Potato seed pieces	30	2	7	White, rapid.
	5	do	Decaying beans	11	2	18	Slow, dark.
	6	do	Laboratory [2]	6	1	17	White, rapid.
1931	1	do	Potato seed pieces	38	0	0	None.
	2	do	Reared in laboratory [3]	14	1	7	White, rapid.
			Overwintered in field				Slow, dark.
1932	1	Adult	Captured in field	22	2	9	Dark, slow.
	2	Larva	Potato seed pieces	4	0	0	None.
	3	Pupa	Late blight tuber decay	32	2	6	White, rapid.

[1] The different cultures isolated from the respective insects were tested for pathogenecity on potato slices in moist chambers.

[2] From insects used in laboratory infection studies recorded in table 4.

[3] Pupae reared in the laboratory and later overwintered in the soil in the field.

Bonde (*2*) in previous studies isolated soft rot bacteria from within the puparia of the seed-corn maggot. As shown in table 1, pathogenic bacteria were secured from the pupal stage in each of the five seasons in which the studies were conducted. Puparia containing pathogenic bacteria were obtained from the vicinity of potato tubers decayed by the late blight fungus and by secondary organisms.

The insects used in the infection studies (table 4) were secured from the field and produced blackleg and bacterial decay under controlled laboratory conditions. The pathogenic organisms isolated from these puparia were tested further on potato plants and found capable of causing blackleg.

As shown in table 1, the adult *Hylemyia cilicrura* may harbor pathogenic bacterial organisms. Leach concluded that the digestive tract of the adult insect contains the soft-rot bacteria and that the eggs in the process of oviposition are contaminated. The fact that the writer secured the organism from the surface of eggs deposited in sterile soil confirms this conclusion.

The writer has not isolated pathogenic organisms from the larval stage of *Hylemyia cilicrura*. His tests were, however, very limited and are not conclusive.

Isolations were made from the different stages of the seed-corn maggot reared in the process of experiments conducted in Charleston, S. C., during the potato-planting season of 1930. These isolations (table 2) were generally in accord with the results secured from the Maine studies.

One pathogenic bacterium isolated from a puparium reared in the laboratory is of particular interest. Maggots penetrated potato seed pieces planted in sterilized soil and produced an active decay. The pathogenic organism associated with this decay was reisolated from within a puparium reared from this material. This bacterium was found to be very actively pathogenic and capable of producing seed-piece decay and blackleg in the potato.

TABLE 2.—*Isolations of pathogenic bacteria from the different stages in the life cycle of the seed-corn maggot, Charleston, S. C., 1930*

Stage of insect	Source	Pathogenicity of cultures		
		Total	Pathogenic	
		Number	*Number*	*Percent*
Egg	Deposited in sterile sand	17	3	17.6
Adult	Reared from laboratory infection experiments	11	2	18.1
Pupa	Decaying seed potatoes from field	21	4	19.0
	Decaying spinach (*Spinacia oleracia* L.)	11	0	0
	Decaying chickweed (*Stellaria media*)	2	1	50.0
	Reared from laboratory infection studies in sterile sand	17	1	5.8

The data in tables 1 and 2 have been summarized in table 3. Approximately 7 percent of the eggs, 15 percent of the puparia, and 10 percent of the adults harbored bacteria capable of rotting potatoes. The percentage of the insects containing pathogenic bacteria probably depends to a large extent on the type of rotting material in which the larvae fed. In some types of decay in which the bacteria are mostly saprophytic none of the insects may be carriers of pathogenic organisms. On the other hand, if the larvae have been feeding on material

decayed by the soft-rot bacteria, a high percentage of the insects may contain pathogenic bacteria.

All of the insects studied yielded, in addition to the pathogenic bacteria, an abundance of saprophytic bacteria of several kinds. None was free from microorganisms.

TABLE 3.—*Summary of pathogenic organisms isolated from the different stages in the life cycle of the seed-corn maggot*

Stage of insect	Total eggs or insects	Eggs or insects yielding pathogenic organisms	
	Number	*Number*	*Percent*
Egg	43	7	16.3
Larva	4	0	0
Pupa	257	38	14.8
Adult	95	9	9.5

BACTERIA AS A FACTOR IN THE NUTRITION OF THE SEED-CORN MAGGOT

The writer has not made a detailed study of the nutritional requirements of the seed-corn maggot. This problem has, however, a direct bearing on the feeding habits of the insect as related to injury to potato seed pieces. Leach (*12*) showed that sterile maggots were not able to develop on sterile potato tubers but grew normally when bacteria were added. Huff (*6*), who made a more detailed study of the nutritional requirements of the seed-corn maggot, found that the larvae would not grow to maturity on sterile beef-extract agar or potato plugs. When the agar or the potato plugs were contaminated with bacteria the maggots grew normally. He was unable to grow the larvae on bacteria-free filtrate from unheated potatoes or on sterile potato to which had been added a suspension of bacteria killed by heat; on the other hand, the larvae grew normally on potato plugs, beans, and peas that had been partly decomposed by bacteria and then sterilized by heat. Huff concluded that the bacteria per se are not essential for the development and pupation of this insect but that they convert plant tissue into available food for the larvae. Huff was able to rear the maggots at a normal rate of development on sterile bean and pea seedlings. Leach (*15, p. 402*) found that larvae would develop faster and a higher percentage would reach maturity if the seedlings were contaminated with bacteria.

The exact role of the bacteria found associated with the feeding larvae is not known. The writer has attempted to rear sterilized larvae on sterile potato-dextrose agar, beef-extract agar, and sterile cooked peas, beans, and cabbage. None of the attempts with these media were successful. The larvae also failed to develop normally on pure cultures of *Erwinia carotovora*, *Phytomonas campestris*, and *P. lachrymans* grown on the above-mentioned substrata. The larvae grew to some extent on the inoculated media, but in no case was the development rapid; and only a few puparia were formed when pure cultures of bacteria were employed.

The addition of a slight amount of unsterilized soil from the field greatly hastened the development of the larvae. When unsterilized soil was added to the different media in flasks in which the pure bacteria were growing, bacterial contamination occurred and thereafter

practically 100 percent of the eggs and larvae developed to the adult stage. The amount of soil added was too small to seem to have any direct nutritive value. These results indicate that certain other soil organisms found in association with the soft-rot condition are essential for the normal growth and development of the seed-corn maggot.

INOCULATION STUDIES WITH THE SEED-CORN MAGGOT AND SEED-POTATO MAGGOT

No evidence is available to show that the flies of the seed-corn maggot infect potato seed pieces by direct contact. The flies are often seen resting on and about seed pieces that have been left exposed in the furrow, but there is no proof that bacterial rots have resulted from such association. Observations both in Aroostook County, Maine, and at Charleston, S. C., failed to show that the adult of *Hylemyia cilicrura* Rond. frequents the potato bin. The writer has never seen a specimen of the adult in a potato bin or storage house, although he has made a special effort to observe adult flies about storage houses. Experiments were made to test the ability of *Hylemyia cilcrura* and *Hylemyia trichodactyla* to inoculate potato seed pieces by contact in the field.

STUDIES IN MAINE

Adult anthomyiid insects were captured in the field by means of wire-screen traps baited with moistened fish meal (fig. 2).[4] [5] The insects were then transferred to glass jars containing freshly-cut potato seed pieces partly covered with sterilized soil; for most of these studies from 5 to 10 adult insects were introduced into each jar with the seed piece, except in 1930 when a single fly was used in each jar. The seed pieces used in the studies of 1929 and 1930 were inoculated with pure cultures of *Alternaria solani* before being sub-

TABLE 4.—*Inoculation of potato seed pieces with adult insects in the laboratory*

Year	Experiment[1] No.	Insect used	Development insects	Total seed pieces	Results of inoculation		
					Black-leg	Decay	Healthy
				Number	*Number*	*Number*	*Number*
1927	1	*Hylemyia cilicrura*	Larvae numerous	5	4	1	0
	2	do	do	5	2	3	0
	3	do	do	5	4	1	0
	4–8	do	None	25	0	0	25
	9	*Drosophila* sp	do	5	0	0	5
	10	do	do	5	0	0	5
	Controls	None		10	0	0	10
1928	1–18	*Hylemyia cilicrura*	None	90	0	0	90
1929[2]	1–11	do	Larvae numerous	55	22	22	11
	12–36	do	None	125	0	0	12
	Controls	None		5	0	0	55
1930[2]	1–5	*Hylemyia cilicrura*[3]	Larvae present	25	10	0	15
	6–10	do	None	25	0	0	25
	11	*Hylemyia trichodactyla*[3]	Larvae present	5	1	1	∞
	12–13	do	None	10	0	0	10
	Controls	None		10	0	0	10

[1] 5 seed pieces were included in each test.
[2] Seed pieces were inoculated with cultures of *Alternaria solani* and then transferred to the jars of sterilized soil with the insects.
[3] 1 female fly was used for each jar.

[4] The identification of the insects was kindly verified by Dr. O. A. Johannsen of Cornell University, Dr. H. C. Huckett of the Long Island Vegetable Research Farm, Riverhead, N. Y., also rendered aid.
[5] The technique for obtaining flies of the seed-corn maggot was adopted from that used by W. J. Reid. The writer is indebted to him for help and courtesies shown in Charleston, S. C.

jected to the attack of the insects. This fungus was used because it causes shallow and superficial lesions on potato slices, and because such lesions attract the maggots. After shallow lesions had been formed by the fungus, the seed pieces were transferred to jars of sterilized soil, before the flies were introduced. The soil was kept

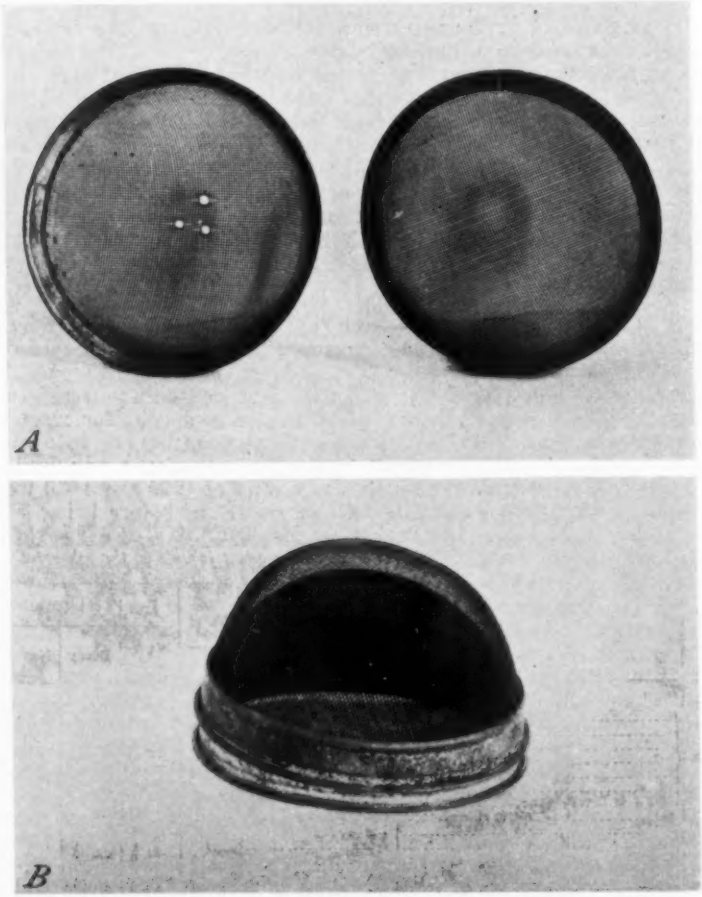

FIGURE 2.—Cage used for catching the adult of the seed-corn maggot in the field: *A*, Trap unassembled; *B*, trap assembled. These traps were baited with fish meal and set in the fields frequented by the insects.

moist by artificial watering. The temperature varied in the laboratory from 10° to 18° C. The results are summarized in table 4.

In 1927 daily observations were made for a period of about 8 days with no obvious decay being apparent. After approximately 21 days decay was present in 3 of the 8 jars. The rotted seed pieces,

contained numerous maggots of *Hylemyia cilicrura* which were actively feeding and burrowing into the potato tissue, and 5 of the 15 seed pieces disintegrated before plants were developed. The other

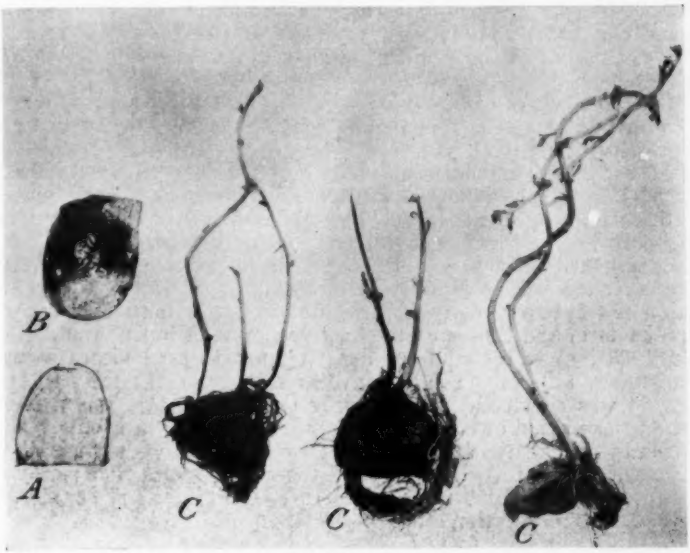

FIGURE 3.—Plants with the blackleg disease produced by inoculation with the seed-corn maggot in jars of sterilized soil: *A*, Healthy control; *B*, decayed seed piece showing maggots; *C*, diseased plants from which the blackleg organism was isolated.

FIGURE 4.—Bacterial decay induced into healthy seed pieces by the seed-corn maggot. The healthy seed pieces were planted in jars of sterilized soil and the insects that had been caught in the field introduced.

10 seed pieces, less severely attacked by the soft-rot organism, produced plants with typical blackleg (fig. 3). Figure 4 depicts a bacterial decay induced in healthy seed pieces in a similar experiment,

also using the seed-corn maggot. Isolations were made from these affected plants, and a white-rot organism capable of producing the blackleg disease was obtained. The control seed pieces from the same tubers remained sound until discarded late in the season.

In the five jars (Nos. 4–8) in which decay failed to develop, the adult insects perished. Larvae were produced but were unable to penetrate the tissues of the healthy seed pieces and therefore died in an early stage of development.

In 1928 all of the 18 insect inoculations gave negative results.

The experiment was repeated in 1929. The results are given in table 4.

In these infection studies inoculated seed pieces oftentimes failed to decay and produce diseased plants. There may be several reasons for these failures: Some of the flies apparently were infertile when captured in the field; moreover, maggots seldom attack seed pieces unless bacterial lesions or a superficial decay are present. The reasons for this will be explained later. Also, as shown in a preceding section of this paper, many maggots are not contaminated with pathogenic bacteria and thus are not effective agents of inoculation.

In 1926 insects reared from decaying potato seed pieces secured from different fields were all identified as being *Hylemyia trichodactyla*. It was concluded that possibly this species also was a factor in the transmission of seed-piece decay and blackleg in Maine.

Examination of the insects caught by sweeping with a net about gardens and fields revealed that often these two species of anthomyiids was obtained. In 1930 it was decided to use individual female flies for the insect-inoculation studies.

The data obtained from a series of inoculation experiments with individual flies in 1930 are recorded in table 4. The data, although not very extensive, indicate that *Hylemyia trichodactyla* is also capable of introducing the soft-rot bacteria into healthy potato seed pieces and thus initiating blackleg.

Studies in Charleston, S. C.

During the planting season of 1929 and 1930 the writer studied blackleg and seed-piece decay in the vicinity of Charleston, S. C., where conditions are quite different.

Freshly cut seed pieces from surface-sterilized Irish Cobbler tubers were divided into several lots and exposed to flies in the field. The seed pieces of one lot were placed directly in an open furrow in the soil, those of another lot were placed in the open field on previously disinfected papers to avoid contamination from the soil, while the controls were maintained in covered containers. The seed pieces were exposed to fly infection for a period of 7 hours and then removed to damp chambers for incubation.

The weather was warm (about 15° C.), the sky cloudy, and the humidity high, a set of conditions that should have been favorable for the development of decay. Although 100 seed pieces were exposed to an abundance of flies, no decay was observed as a result.

Surface-sterilized tubers were broken open and exposed to flies of *Hylemyia cilicrura* in the fields under ideal conditions for rot as previously described. When several flies had settled and had walked

over the freshly opened potato surfaces, the tuber parts were closed and held together with the aid of rubber bands and placed in damp chambers. No decay resulted in the 45 tubers thus treated.

Adult insects were trapped in a freshly planted potato field and transferred to insect cages set over sterilized pans of soil in the laboratory. Figure 5 shows an insect cage of the type used. The eggs were removed by means of a fine camel's-hair brush to freshly cut potato slices in 2 sterilized Petri dishes. Approximately 10 eggs were used for each inoculated potato slice. The eggs hatched within a few hours, and the small maggots soon burrowed out of sight into the potato tissue. Rot developed in the potato slices inoculated in this manner. Several days later, potato slices in three additional Petri dishes were inoculated in a similar manner using a different lot

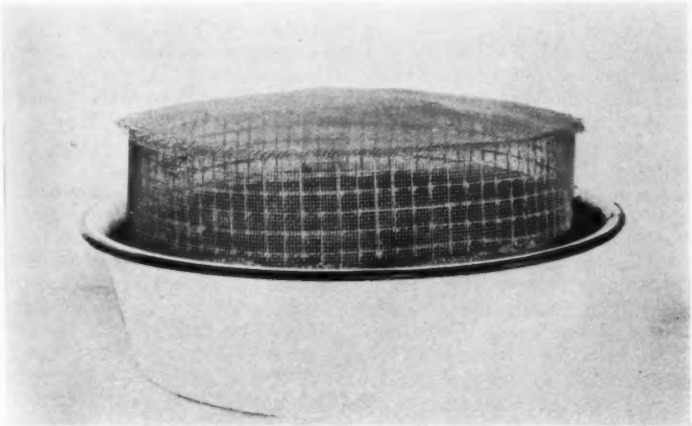

FIGURE 5.—Type of cage employed for inoculation studies using the seed-corn maggot. The adult insects were enclosed over pans of soil containing potato seed pieces.

of eggs. A rapid, soft rot also occurred in these potato slices. Toward the end of the planting season still another lot of potato slices was inoculated with eggs transferred from sterilized soil. This lot also was decayed by bacteria. No bacterial decay occurred in the uninoculated control potato slices. The results of these experiments are given in table 5 (lot 1).

In these inoculation experiments it was found desirable to keep the eggs quite moist. This was done by covering them with a bit of agar or with a moistened cover slip. The inoculations were also more successful if five or more eggs were used for each slice instead of a few or individual eggs.

Subinoculations of additional potato slices in moist chambers were made with the bacteria secured from these egg inoculations, with positive results. Pure cultures were also obtained of those found capable of causing blackleg. These cultures were identified by morphological and physiological characteristics as of the blackleg pathogen.

TABLE 5.—*Inoculation studies with the seed-corn maggot in Charleston, S. C.*

Lot No.	Sublots [1]	Stage of insect	Source of insect	Material inoculated	Type of decay
1	A–F	Egg	Cropped field	Potato slices in sterilized Petri dishes	White, soft.
2		Young larva	Rotted seed pieces from field.	Sterile potato slices in moist chambers	Do.
3	A–B	Adult	Cropped field	Freshly cut seed pieces in unsterilized soil.	Do.
	C	do	do	do	White, soft; also yellow.
4	A	do	do	Freshly cut seed pieces in sterilized soil.[2]	Rapid, yellow.[3]
	B–C	do	do	do	White, soft.[3]

[1] 5 slices or seed pieces were used in each sublot, which was tested at a different time from the others in the same lot.
[2] The soil was sterilized with dry heat.
[3] Rot developed in only 1 seed piece in each of the 3 pans.

Studies in Maine had shown that maggots taken from decaying potato seed pieces were capable of transmitting this decay to other seed pieces provided no protective cork layer had been formed. When maggots introduced the rot-producing organism into freshly cut seed pieces, an active decay resulted provided the soil was moist. Similar studies were made with the larval stages in South Carolina. Young maggots were removed from the interior of field-infected seed pieces, placed in freshly cut potato slices in moist chambers, and covered with moist, sterilized sand to prevent excessive drying. These inoculations resulted in an active decay (table 5, lot 2) which, when pricked into healthy potato sprouts, produced blackleg. Nine single-colony, pure-culture isolations were thus secured; all of the isolations belonged to the soft-rot group of bacteria.

The data show that the young larvae are more active and are better inoculating agents than the more mature maggots. As the maggots mature, they become sluggish and do not penetrate deeply into the potato tissue and thus are not very effective in causing the destruction of potato seed pieces. The maggots rarely, if ever, migrate to another seed piece after they have once penetrated a seed piece. This is especially true as they reach maturity. For this reason it is very unlikely that the maggots spread decay from one seed piece to another.

Additional experiments were made to determine more definitely to what extent larvae of the seed-corn maggot introduce pathogenic bacteria into healthy seed pieces.

In these experiments freshly cut surface-sterilized Irish Cobbler seed pieces were planted in pans of moist soil taken directly from the field, in comparison with similar seed pieces planted in sterilized soil. The pans were covered with insect cages, and adult insects were introduced as in the previous experiments. The freshly cut seed pieces planted in the unsterilized soil were severely attacked by the maggots resulting in decay (table 5, lot 3), which was particularly rapid and destructive when the soil was moist. The control seed pieces, which were allowed to suberize for 2 or 3 days and then planted in the unsterilized soil, remained entirely free from all maggot attack and bacterial decay. The factor of suberization will be discussed more fully later.

The injury from maggots and rot was greatly reduced in the studies with sterile soil, and only one seed piece in each of three pans of soil was injured (table 5, lot 4). None, or very few, primary lesions were present on the cut surfaces of the seed pieces in the sterile soil, and many of the young maggots perished for lack of suitable food. Apparently they had difficulty in attacking the healthy suberized potato tissue.

The decay organism was isolated in pure form from about the tunnels made by the feeding larvae. These cultures were similar to the soft-rot and yellow-rot organisms previously isolated from seed pieces taken from the field that were decayed or infected with maggots.

In view of the fact that the experiments (table 5, lot 4) were conducted under controlled conditions with the use of disinfected seed pieces and sterilized soil, the writer feels that it has been demonstrated that the adult of the seed-corn maggot is a carrier of the pathogenic bacteria. The results obtained in South Carolina studies support the data in the Maine studies.

INFLUENCE OF VARIOUS FACTORS ON INSECT INFESTATION AND DECAY OF POTATO SEED PIECES

INFLUENCE OF LESIONS CAUSED BY PHOMA TUBEROSA, FERTILIZER INJURY, AND DIFFERENT BACTERIA

The writer has noted that seed-piece decay by *Phoma tuberosa* and by *Fusarium* sp. is extremely common and that lesions caused by these fungi may contain pathogenic bacteria. The seed pieces affected in this manner generally are responsible for both missing hills and blackleg in abundance. Bacteria capable of producing blackleg often have been isolated from this source.

Seed-piece decay and blackleg were associated also with injury caused by fertilizer burning in the soil at planting time.[6] The decayed seed pieces often contained numerous insects including the seed-corn maggot and the seed-potato maggot, as well as certain species of *Staphilinidae*, and the larvae of the larder beetle (*Dermestes lardarius*).

The fact that spotting by *Phoma tuberosa* and injury to the planted seed pieces by fertilizer were associated with the blackleg disease and with seed-piece decay, made it desirable to test the possibility of a relationship between these troubles and infestation by the seed-corn maggot.

FIELD STUDIES

Tests were conducted during 1930 in the field at Presque Isle, Maine. Seed pieces, infected recently with *Phoma* alone, injured by fertilizer, or affected with bacterial lesions on the cut surface, were exposed to attack by the larvae of *Hylemyia cilicrura* and *H. trichodactyla* under natural field conditions. The seed pieces affected with *Phoma* were selected from a bin of cut seed on Aroostook Farm. The fertilizer injury was induced by lightly sprinkling the cut surfaces of the pieces with commercial fertilizer before planting them in the soil. The seed pieces with bacterial lesions were secured from a bin of affected seed. The lots of seed were all from the same general Green Mountain stock and were grown in fields free from blackleg; the disease, therefore, could not have come from the parent stock.

[6] Seed-piece injury caused by fertilizer burning appears to be less frequent since more modern planters have been developed.

The results are summarized in table 6. The data show certain relationships that may exist between the type of seed-piece spotting and the degree of attack by the seed-corn maggot.

TABLE 6.—*Insect injury and blackleg resulting from seed pieces affected with spotting by* Phoma tuberosa, *by bacteria, and by fertilizer injury, 1930*

Kind of seed	Treatment prior to planting	Seed pieces	Blackleg resulting from treatment	Prevalence of maggots in seed pieces
		Number	*Percent*	
With *Phoma* lesions.	Exposed to adult insects for 30 minutes in furrow.	115	0.0	None.
	Moistened and covered immediately.	100	.0	Do.
	Covered immediately	200	.0	Do.
Freshly cut	do	200	.0	Do.
	Injured with fertilizer	200	1.5	Some maggots in all seed pieces.
Suberized	do	100	2.0	None.
	Not injured with fertilizer	100	.0	Do.
With bacterial lesions.	Commercial storage; planted May 18, 1930.	100	62.0	Abundant.
From same lot as preceding, but free from lesions.	do	100	3.0	Maggots only in 3 seed pieces having decay and blackleg infection; no maggots in healthy seed pieces.
With bacterial lesions.	Commercial storage; planted May 22, 1930.	100	45.0	Abundant in all seed pieces showing decay.

The insects failed to attack the healthy seed pieces or those having only *Phoma* infection before planting. The bacterial lesions in contrast were very attractive to the insects, and each seed piece affected with bacterial spotting when planted later contained many maggots. Both the seed-corn maggot and seed-potato maggot were present in the affected seed pieces. Lesions induced by fertilizer injury also attracted the maggots. The degree of infestation following fertilizer injury was, however, much less than that resulting from infection by bacterial pathogens and the amount of blackleg was relatively small.

In 1930 an attempt was made to create a blackleg epidemic by injuring seed pieces with fertilizer. Seed pieces were dusted with fertilizer and covered with soil in the field. All of the seed pieces injured in this way became infested by *Hylemyia cilicrura*, whereas the uninjured controls were not. The maggots in each case entered through the tissue rendered soft by the toxic effect of the fertilizer.

The tests of 1930 were repeated during 1931 and 1932. The amount of blackleg resulting from these insect inoculations was very small, however, never being more than 1 or 2 percent. The writer does not feel that all of the blackleg that occurs in northeastern Maine can be attributed to inoculation by the seed-corn maggot. Other factors often determine the amount of infection.

In further tests, healthy potato tubers were cut in halves with a sharp knife and the freshly cut surfaces inoculated by streaking them with a soft-rot bacterial culture. The inoculated tubers were incubated in the laboratory for 1 day and then planted in the field. Each inoculated tuber part was alternated, when planted in the field, with a freshly cut, uninoculated control. In one experiment two plantings, each consisting of 100 inoculated tubers, were made, one on June 5 and the other on September 15.

The inoculated tubers and their control were examined for maggot injury at different intervals. No maggots were found in the uninocu-

lated controls, while 60 of the inoculated tubers planted on June 5 contained maggots, and 25 of those planted on September 15 were thus infested. The adults reared from the larvae in this experiment were of *Hylemyia trichodactyla*.

Laboratory Studies

The role played by bacterial lesions in the degree of infestation of potato seed pieces by insects was tested further by experiments in the laboratory.

Irish Cobbler tubers free from bruises and blemishes were selected. Two notches in close proximity to each other were made with a sharp

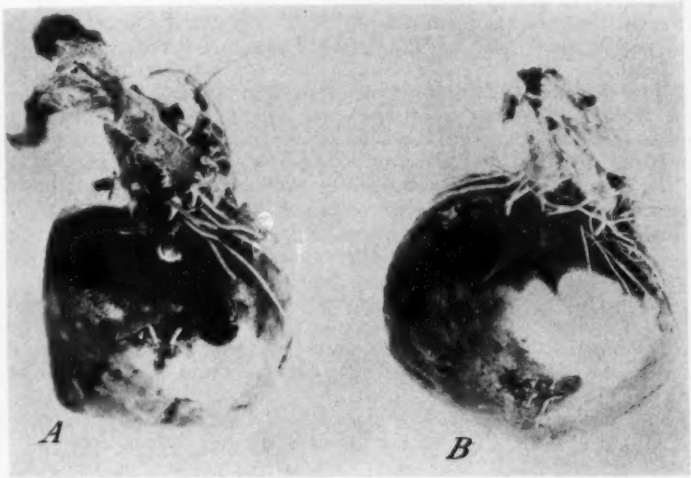

Figure 6.—*A*, Maggot attack in seed piece in area previously inoculated with a soft-rot culture; *B*, absence of attack in a similar seed piece that had not been contaminated with pathogenic bacteria. Both seed pieces were included in the same pan experiment in the presence of insects. Surface of seed pieces removed to show the extent of the decay.

knife through the periderm of the tuber. The freshly cut tissue of one of these notches in each tuber was inoculated with a soft-rot culture and the other notch was left uninoculated as a control. The tubers thus treated were planted in shallow pans of moist soil and kept in the laboratory.

Adult insects, trapped in the field, were brought to the laboratory and confined over the pans of soil in which seed pieces were planted. From 35 to 50 insects were used for each pan. Seven lots of seed each containing 10 seed pieces were subjected to insect attack.

The flies confined with the pans of potatoes deposited eggs in the moist soil in great numbers, and the young maggots began to hatch soon after the first day. The young larvae began to migrate in the soil in search of food and were found to enter the potato tubers only through the notches that had been inoculated with the soft-rot bacteria (fig. 6). This experiment shows that maggots are attracted by

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bacterial decay and will migrate to such bacterial lesions. Under good growing conditions such small lesions would usually heal without destroying the seed piece; but when attacked by maggots the seed pieces are generally destroyed, and if a plant is formed it may develop blackleg.

Studies in Aroostook County, had led the writer to suspect that the source of seed-piece decay in the South was in the storage bin. Contrary to expectation, the unplanted seed lots observed in the Charleston area were exceptionally free from decay of all sorts, although information gained through conversation with growers would indicate that decay sometimes occurs. Very few decayed or injured seed pieces were found before planting, and the rots which followed after planting could hardly be attributed to bin contamination. This fact indicates that the problem of seed-piece decay and uneven stands as observed in the vicinity of Charleston, is somewhat different from that in Maine.

When healthy seed pieces were planted in soil from the Charleston area, it was noted that small bacterial lesions often developed on the cut surfaces and the seed pieces often contained numerous small maggots. Further field observations revealed the fact that the association of maggot injury with lesions was quite general and that this insect rarely attacked a firm and healthy seed piece.

A series of laboratory experiments were made in order to study this relationship. Ten seed pieces affected with small, superficial lesions were removed from the field and replanted in moist soil in pans in the laboratory along with seed pieces free from all evidence of decay. The healthy and the spotted seed pieces were alternated in the soil so as to compensate for any place effect. Approximately 30 flies captured in the field were enclosed with the pans and allowed to deposit their eggs in great numbers.

The pans were kept well moistened in subdued light at approximately 15° C. for 5 days before being examined. The results of this simple test were very striking. The eggs deposited by the flies had hatched in great numbers, and the young larvae had migrated to the seed pieces. The seed pieces affected by the shallow surface lesions had been greatly injured and in some cases were practically destroyed by maggot attack. The healthy seed pieces, in contrast, remained firm and bright and produced healthy vigorous sprouts. This experiment was repeated with similar results.

INFLUENCE OF SOIL BACTERIA

It was shown in the preceding experiment that maggots attacked seed pieces having superficial lesions that resulted when the potato sets were planted in the field under the conditions of Charleston. This indicated that the pathogenic soil organisms abundant in such soils might greatly influence the infestation of seed pieces by the seed-corn maggot. An experiment was made with the view of answering the question. Freshly cut seed pieces and suberized controls were planted both in sterilized soil and in soil taken directly from the field. Adult insects captured in wire-screen traps in the field were confined with the planted seed in the two kinds of soil. The soil was kept well watered and at a temperature of approximately 15° C. for the duration of the test. Each treatment was made in

duplicate, and examinations of the seed pieces were made at different intervals.

TABLE 7.—*Seed-piece decay and maggot injury in sterilized and unsterilized soil* [1]

Lot No.	Treatment of seed	Adult insects added [2]	Seed-piece decay and insect injury—	
			In sterilized soil	In unsterilized soil
		Number		
1	Freshly cut	0	None	Surface lesions on all seed pieces.
2	Suberized [3]	0	do	None.
3	Freshly cut	0	do	All seed pieces badly decayed.
4	do	30–35	do	Severe insect injury in all seed pieces; complete decay.
5	do	30–35	3 seed pieces were penetrated by maggots; 2 of these developed rot.[4]	Do.
6	Suberized [3]	30–35	None	None.

[1] Each lot contained 30 seed pieces. The soil was sterilized by dry heat.
[2] Adult insects trapped in the field removed to the laboratory. The adults deposited eggs in great numbers in the soil. The eggs hatched within 12 to 24 hours and immediately migrated to favorable sources of food.
[3] Suberized by being placed in moist chambers for a period of 5 days.
[4] The maggots attacked the seed pieces slightly on the cut surfaces. Each rotted seed piece contained approximately 20 small maggots, all of which had entered at 1 small hole, probably originally a small lesion. The soft rot organism (*Erwinia carotovora*) was isolated from this material, demonstrating further that the seed-corn maggot may introduce pathogenic bacteria into potato seed pieces.

The results of this experiment are summarized in table 7. Seed pieces previously suberized for 5 days in moist chambers at 15° C. remained healthy and free from all insect injury in both sterilized and unsterilized soil; also, no lesions developed on freshly cut seed pieces planted in the sterilized soil free from insects. On the other hand, the freshly cut, unsuberized seed pieces planted in unsterilized soil all developed decay in various degrees of severity. The severity of the decay apparently depended on the amount of soil moisture present. The injury by the seed-corn maggot was also very extensive.

Freshly cut seed pieces planted in sterilized soil were not spotted and escaped attack by insects. However, the maggots penetrated three seed pieces apparently free from externally obvious decay. Two of the seed pieces thus attacked later developed an internal bacterial soft rot, with only a very small opening to the outside. The maggots apparently had entered in quite large numbers through a relatively small opening caused by bacteria introduced by the adult insect on the eggs.

The seed pieces planted in sterilized soil that were attacked by the seed-corn maggot yielded pathogenic bacteria, later identified as belonging to the blackleg or soft-rot group. Since the soil and the seed pieces were sterilized before planting, there can be no doubt that the organisms were introduced by the insects.

This experiment shows that the potato soils in the vicinity of Charleston contain pathogenic bacteria that are capable of injuring the planted potato sets. These soil bacteria often determine the success of the attack on potato seed pieces by the seed-corn maggot. The fact that soft-rot bacteria were isolated from seed pieces planted in sterilized soil is also significant. It shows that pathogenic bacteria may in some cases be introduced by the seed-corn maggot.

An experiment was also made which showed that the lesions resulting in the field and those produced in the laboratory were similar. Both were caused by the soft-rot bacteria (*Erwinia carotovora*) and by

an unnamed bacterium possessing polar flagella and capable of causing a yellow rot in potato seed pieces.

In the fields about Charleston the lesions result from infection originating in the soil. The larvae of *Hylemyia cilicrura* enters the seed pieces through these superficial lesions and penetrate deeply into the tissues, preventing the tubers from healing and hastening the decay. In Maine both the seed-corn maggot and the seed-potato maggot are attracted by bacterial lesions. Primary infection in Maine, however, generally occurs before the seed is planted in the soil.

EFFECT OF EXCESSIVE EARLY DRYING OF SEED PIECES

Field Studies

In another series of experiments it had been noted that missing hills and seed-piece decay were correlated with injury of the cut seed by excessive early drying prior to planting. The injury consists of a drying and killing of the surface layers of cells because an adequately protective new cork layer failed to form. It was not known, however, whether this drying increased the amount of infestation by insects. In order to gain this desired information, seed pieces injured by such drying were exposed to maggots in the field in comparison with healthy controls and the relative degree of injury was noted.

The Irish Cobbler variety was used. Whole tubers that were free from all evidence of disease and bruises were each cut into 4 seed pieces of equal size, 2 of these were exposed for 1 day in the bright sun and drying wind, while the other 2 were stored in a cool basement until planted. The seed pieces exposed out of doors became somewhat shriveled and darkened on the cut surfaces while those stored in the basement remained bright and firm. The 2 lots of seed were alternated in the row when planted in the field. Each lot consisted of 100 seed pieces, and planting was made on three different days, May 20, June 5, and June 10. The lots were examined at different times during the season and the degree of injury by insects was noted. The decay that developed was 10, 55, and 30 percent, respectively. No maggot infestation occurred in the seed pieces planted May 20, whereas the maggot infestation of the planting on June 5 was 40 percent that of June 10, 28 percent. No decay or maggot infestation was observed in the controls.

Early exposure to sunlight and dry air therefore may result in a high percentage of maggot infestation and decay in the planted seed pieces. This generally results in poor stands. Plants that survive such treatment may be small and weak and yield poorly. Many of the uneven stands found in the potato-growing areas occur because of this type of injury. In no case in this experiment was a firm and healthy seed piece attacked by these insects. The insects in these tests were mostly *Hylemyia trichodactyla* Rond. Bushnell (*4*) pointed out that poor potato stands in Ohio may result from injury to cut surfaces from exposure to sun and wind and reported that an exposure of more than half an hour greatly reduced the percentage of plants that emerged from the soil. He does not mention whether the practice results in an increase of insect infestation.

Laboratory Studies

The effect of drying and sunlight on the amount of seed-piece decay and maggot infestation was tested also in the laboratory. Potato seed pieces were injured by exposure to direct sunlight and dry air. Five seed pieces thus injured were planted in pans of soil with five healthy freshly cut seed pieces, making 10 in each pan. Flies were introduced from the field and were confined over the pans. The seed pieces were examined after the maggots had developed and begun to feed. Seven lots of seed pieces were used.

The data obtained support the conclusion that early exposure of freshly cut seed pieces to sunlight and dry air favors attack by the

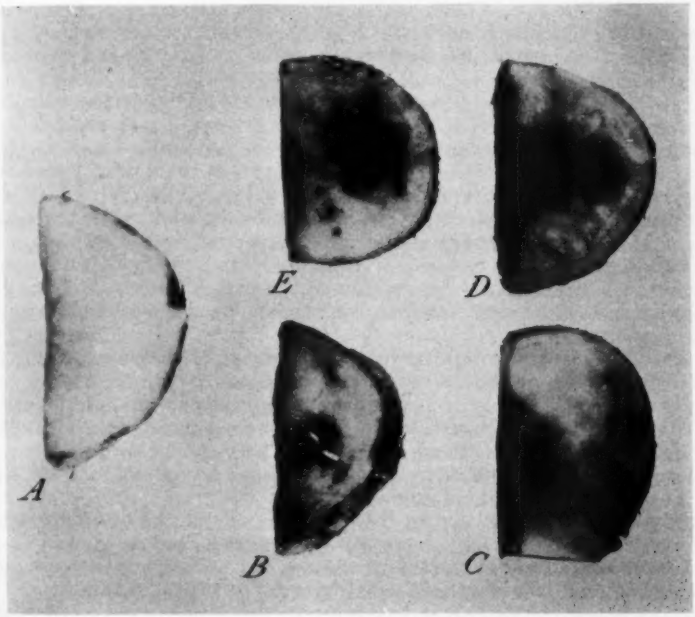

Figure 7.—Maggot injury resulting in the field in seed pieces that had been injured by exposure to dry air before being planted: *A*, Control seed piece that was not injured by drying and was not attacked by the maggots; *B–E*, injured seed pieces. Note the maggots in *B*.

maggot. No insects were found in the healthy seed pieces. The injured seed pieces, on the other hand, were in the majority of cases badly decayed and were infested with larvae of both *Hylemyia cilicrura* and *H. trichodactyla*. Figure 7 shows maggot attack on seed pieces injured by excessive drying. In these tests the seed-potato maggot was most commonly encountered although the seed-corn maggot also was present.

INFLUENCE OF SOIL MOISTURE

The initiation of seed-piece spotting and decay is influenced by the amount of soil moisture. This fact suggested that decay in seed pieces following infestation with maggots might be influenced in a similar manner. The writer, in his isolations from seed pieces injured by maggots, was often able to secure pathogenic bacteria from the region about the wounds made by the seed-corn maggot in spite of the fact that no decay was obvious. It would seem that these latent bacterial infections should cause a more rapid decay under the right environmental conditions.

Leach (*14*) has shown that tubers held under moist conditions are unable to form a protective wound-cork layer. According to his data (*14, p. 224*) the tubers were only slightly suberized when the moisture content in sand was from 12.03 to 12.59 percent (of dry weight) and the protective layer failed to develop entirely when the soil moisture was 14.75 percent.

Freshly cut seed pieces were subjected to attack by young maggots in the laboratory. After maggots had penetrated and burrowed into them, the seed pieces were removed from the pans of soil and divided into two similar lots. One lot thus injured was planted in relatively dry, and the other in relatively moist soil. In the second series, freshly cut seed pieces, free from maggots, were planted in a similar manner. A third set of pans contained suberized seed pieces planted like those in the first two sets. Adult flies from the field were introduced into cages over the freshly cut and suberized seed pieces. Twenty seed pieces were used in each test. Each set of comparisons was repeated.

The seed previously injured by the burrowing of the young maggots was completely destroyed when subjected to the conditions in the moist soil. The same type of injured seed pieces planted in the drier soils developed no apparent decay and sprouted normally. Cultural isolation showed that these seed pieces had been inoculated with pathogenic bacteria but that their growth and advancement into the potato tissue had been checked.

Microscopic examination of freehand sections of the potato tissues subjected to conditions in the moist soil revealed that no wound cork had been formed about the insect wounds. In the dry soil the insect wounds of seed pieces were blocked by a layer of cork tissue.

Leach (*14, p. 224*) showed that a protective layer failed to develop when the moisture content of the soil was 14.75 percent. The dry soil used in the experiments reported here had approximately 6 to 7 percent of moisture and the wetter soil approximately 9 to 10 percent. In no case was the moisture excessive or the soil completely waterlogged and the conditions approximated quite closely those that often exist under field conditions.

The freshly-cut seed pieces planted with flies developed no rot or insect injury in dry soil. In wet soil, however, these unsuberized seed pieces were completely destroyed by a bacterial decay.

The experiments show that when such infested seed pieces are subjected to sufficient soil moisture, the decay becomes rapid and may totally destroy the potato sets. High soil moistures often occur after heavy rains. If unsuberized seed pieces are planted under such conditions they quickly develop the necessary soil lesions for insect attack.

The insects which attack the seed pieces through the lesions may introduce additional pathogenic microorganisms and under the favorable conditions of high soil moisture the seed pieces are rapidly destroyed.

The suberized seed pieces planted in both moist and dry soils developed no decay, nor were they injured by the insects. The seed pieces sprouted normally and produced healthy plants.

RELATION OF WOUND-CORK FORMATION TO ATTACK BY THE SEED-CORN MAGGOT

Reid, Peacock, and Wright found that (*17*) in the trucking area in the vicinity of Charleston, S. C., the injury to planted potato sets caused by the seed-corn maggot could be controlled by proper suberization of the seed before planting. They recommend that seed stock be thoroughly disinfected before cutting and allowed to cork over for a period of 10 days or 2 weeks at a temperature of 55° to 65° F. at a relative humidity of 80 to 90 percent before being planted. Johnson (*10*), however, stated that results in Virginia would seem to justify cutting and planting within a few hours. The growers in his section follow various practices—some cut their seed 2 or 3 days before planting, some few cut the tubers a week before planting, while others cut and plant immediately. Johnson has depicted a field with an exceedingly poor stand which resulted from planting tubers that had been cut and held in storage for 10 days (*10, fig. 33*) and in contrast an excellent stand which resulted from planting freshly cut seed pieces (*10, fig. 34*).

According to Reid et al. (*17*) in the spring of 1921, when the weather was unfavorable for rapid planting along the entire Atlantic seaboard, the injury from attacks of the seed-corn maggot was unusually severe, and as much as 50 percent of the planting in the commercial production areas of the Carolinas was destroyed. That large losses still occur along the Atlantic seaboard because of seed-piece decay can be seen by consulting the more recent market news service records.

As pointed out elsewhere in this paper, in the Charleston truck-crop area freshly cut potato seed pieces often develop small surface lesions when planted, if the soil is moist and unsterilized. It has been suggested that suberization is an aid in preventing the formation of these primary lesions which are quite essential for the attack by the seed-corn maggot.

During the seasons of 1929 and 1930, the writer attempted to imitate, under laboratory conditions, the planting practice of the growers in South Carolina. Freshly cut seed pieces as well as suberized seed pieces were exposed to infection by soil organisms and to attack by the seed-corn maggot. The pans of soil were kept fairly moist and warm so as to be ideal for the germination of the potato sets.

Freshly cut seed pieces in about 24 hours after were examined and planting found to have numerous exceedingly small decayed areas that appeared to be only a few cells in depth and from 1 to several millimeters in diameter. All unsuberized seed pieces planted in unsterilized soil developed these primary lesions in abundance on the cut surfaces, whereas the suberized seed pieces did not. Figure 8 shows these primary lesions.

The seed pieces with the primary soil lesions were replanted in pans of unsterilized field soil in the laboratory. The infected seed

was alternated with seed pieces which had originally come from similar seed stock but which had been allowed to cork over for a period of 4 days in moist chambers. Approximately 30 flies of the seed-corn maggot were taken directly from the field and enclosed by a wire screen with the planted seed pieces.

After a 4-day period the seed pieces were examined. The maggots in great numbers had penetrated the seed pieces affected with the lesions. The corked-over seed pieces, on the other hand, were entirely free from maggot attack. Figure 9 illustrates the maggot injury on the unsuberized seed pieces.

The experiment was repeated with a few variations. Three pans of inoculated seed pieces were used in the second experiment. In

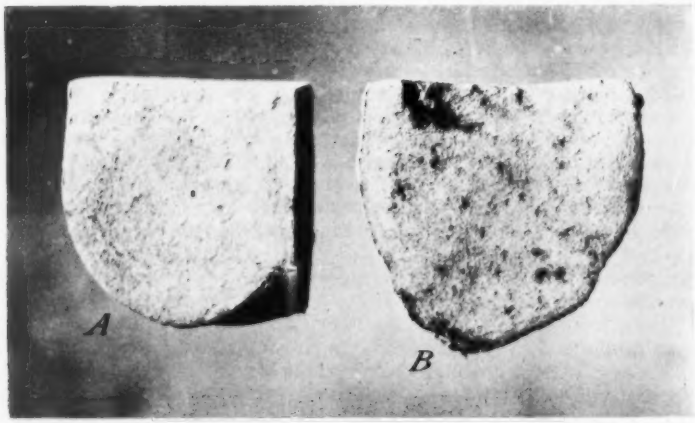

FIGURE 8.—Primary bacterial lesions formed on freshly cut seed piece planted in unsterilized soil from Charleston, S. C.: *A*, Suberized seed piece free from bacterial infection; *B*, unsuberized seed piece with numerous lesions caused by pathogenic soil bacteria. The maggots enter the seed pieces through these superficial lesions.

one pan of unsterilized field soil, 30 to 35 flies were confined with seed pieces having lesions in comparison with seed suberized for only 2 days; in another pan, 20 to 25 flies were confined with seed pieces having lesions in comparison with seed suberized for 4 days; and in the third pan seed pieces that had been suberized for 4 days were compared with spotted seed pieces. No flies were included in the third pan.

The pans were placed in the laboratory at a temperature of approximately 15° C. for the duration of the test. The seed pieces were examined daily and observations made regarding the entrance by maggots.

The larvae began to emerge from the eggs deposited in the soil after 1 day and immediately entered the seed pieces through the lesions induced by soil infection. Entrance was made only through the areas where the potato surface had previously been injured by the pathogenic soil bacteria. The young maggots apparently avoided

all the surface tissue that had a protective cork layer. The seed previously suberized remained entirely free from all decay and produced healthy sprouts. The seed pieces attacked by insects were practically destroyed within 6 days. The seed pieces infected by soil organisms and with no insects present continued to decay. The rot was not rapid, however, for extensive and healthy sprouts developed.

The results of this experiment would indicate that the young larvae of the seed-corn maggot, after having been attracted to the lesions resulting from soil infection, by their tunneling and feeding activities aggravate the infected areas and prevent the natural development of

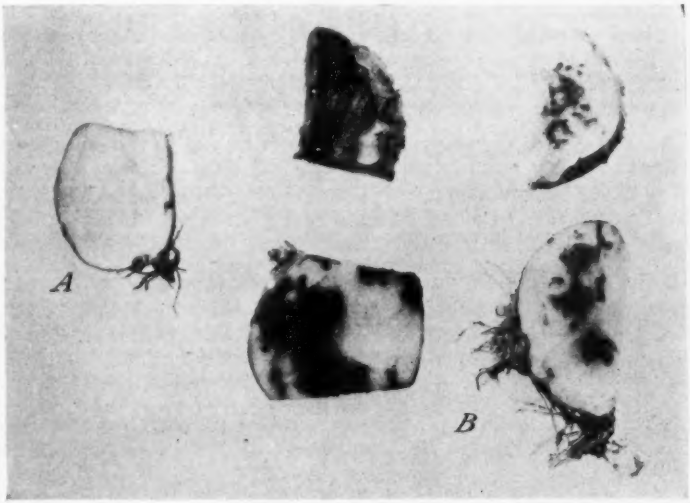

FIGURE 9.—Injury by the seed-corn maggot on unsuberized seed pieces infected from soil containing pathogenic bacteria. The young maggots penetrated the seed pieces through primary lesions similar to those shown in figure 8: *A*, Suberized seed pieces not injured by maggots; *B*, unsuberized and rotted seed pieces with maggot injury. The suberized and the unsuberized, rotted seed pieces were planted in the same pans of soil with the adult insects.

a protective wound periderm, the result being that the seed pieces are destroyed by the pathogenic bacteria.

These studies were continued in South Carolina during the season of 1930 under very similar conditions.

The results of these experiments as well as the general plan of the tests are summarized in table 8. Lesions developed where freshly-cut potato tissue was exposed to moist soil (table 8, lot 1); maggots entered the unsuberized, decayed seed pieces in great numbers, the seed pieces being practically destroyed by their action and by the bacterial decay thus aggravated (table 8, lots 2 and 3). The suberized seed pieces in all cases remained free from decay or insect injury and developed large healthy sprouts. The infested seed pieces, on the other hand, generally failed to germinate.

TABLE 8.—*Comparison of injury by maggots and the extent of decay occurring in suberized and freshly cut potato seed pieces* [1]

Lot No.	Kind of seed piece	Adult flies added [2]	Extent of insect injury	Controls [3]
		Number		
1	Freshly cut [4]	0		Suberized.
2	do	50	Complete destruction	Do.
3	do	40	Severe, followed by decay	Do.
4	Suberized; 1 surface removed with knife.	40	Severe. All injury on freshly cut surface.	Suberized; not cut.
5	Suberized; cork layer broken by freshly cut notches.	25	Maggots entered 2 seed pieces through notches, resulting in decay.	Suberized; not notched.
6	Freshly cut	25	Severe, followed by decay	Suberized.

[1] This experiment was conducted in the laboratory. Each test consisted of 12 seed pieces in addition to 5 controls.
[2] The flies were trapped in the field and transferred to cages covering the pan experiment in the laboratory. The flies deposited their eggs in the soil and the young larvae generally hatched within 12 to 24 hours.
[3] No surface lesions or insect injury in any series.
[4] Numerous surface lesions formed whenever a freshly cut surface came into contact with unsterilized soil.

The importance of suberization to the failure of penetration by the seed-corn maggot was further shown by the data. The surface from one side of the suberized seed pieces was removed and the young maggots migrated to these freshly cut surfaces and entered through the small bacterial lesions that developed there from soil contamination.

In one series (table 8, lot 5) notches were cut with a knife through the suberized surfaces just before planting the seed pieces in moist soil. The small maggots migrated to these injured seed pieces and entered through the notched area where bacteria had initiated rot in small places. The notched seed pieces were found to contain, in some cases, approximately 100 of the insect larvae, and the process of destruction was rapid. In no case was a properly suberized and uncut seed piece injured by maggots or by the rotting soil microorganisms.

These studies show that proper healing of the potato seed pieces eliminates seed-piece spotting caused by soil infection, and this in turn affords a partial control measure for the injury caused by maggots under Charleston conditions.

LABORATORY STUDIES WITH INSECTS OTHER THAN THE ANTHOMYIIDS

In addition to the anthomyiids, discussed in this paper, some of the other insects found commonly associated with potato rots were tested on healthy potato tubers to determine whether they also were capable of introducing the soft-rot organisms and thus could be responsible for the infection that often occurs on seed pieces. The insects tested were the common housefly (*Musca domestica*), the false cranefly (*Trichocera*, sp.), two pomace flies (*Drosophila funebris* Fab. and *D. bruschii* Cog.), the fungus gnat (*Sciara tridentara*), the larder beetle (*Dermestes lardarius*), the wireworm (*Cryptohypnus abbreviata*), and a staphylinid insect.

The tests were made in glass moist chambers located in a cool laboratory basement. The insects in each case were taken directly from the infective material and transferred to the tubers included in

the inoculation tests. In each case many insects were available, and the conditions for rot were ideal so that any failure to secure infection cannot be attributed to the use of too few insect vectors or to unsuitable environmental conditions. With one exception, the insects used in these studies did not inititiate the infection or aggravate the bacterial decay of potato seed pieces. The common housefly (*Musca domestica*), the false cranefly (*Trichocera* sp.), the pomace flies (*Drosophila*), and the fungus gnat (*Sciara tridentata*),[7] although commonly associated with decaying potatoes, apparently act only as scavengers and feed on the decaying organic matter. All of these insects can live and reproduce on decaying potato tissue. The larvae do not, however, penetrate into the healthy part of the potato tuber but remain in those portions that have disintegrated. These insects failed to develop, and in most cases died, when placed in the presence of only healthy potato slices. When decayed tubers were added they developed and reproduced normally.

The larvae of the larder beetle (*Dermestes lardarius*) caused a slight injury to the healthy potato slices in some cases. This injury was quite superficial, however, and no active decay resulted. This insect, in both adult and larval stages, is commonly found feeding on the decayed tissues associated with potato blackleg. It apparently does not disseminate the pathogen of blackleg and seed-piece decay. The larvae of the wireworm (*Cryptohypnus abbreviatus*) readily penetrated the healthy potato slices in these experiments, but no decay was noted as a result of this injury.

The staphylinid was the only kind of insect used in these studies which appeared capable of causing the destruction of potato seed pieces. The larvae of this insect are very active and burrow deeply and beyond the decayed area, in contrast with most of the other insects found in association with seed-piece decay which appear to be merely feeding on the decayed material resulting from the infection. Staphylinids spread the infection by carrying the infective material through the protective cork layer laid down by the potato seed piece. The writer in other experiments has inoculated healthy seed pieces with soft-rot bacteria by means of staphylinid larvae. Pure cultures of the bacterium isolated from seed pieces attacked by this insect have been studied in some detail. The physiological, morphological, and pathological characteristics of this organism place it among the soft-rot group of bacteria.

Observations for several seasons have shown that this staphylinid is exceedingly common in decayed potato material in the field. It is generally present in plants affected with blackleg or seed pieces infected with bacterial or fungus organisms. The writer has found the larvae burrowing in potato stems and seed pieces infected with blackleg. The adults are often seen feeding on infected potato seed pieces.

In no case under field conditions have staphylinids been found to attack seed pieces that had been properly suberized before being planted. Lesions occurring on the cut surfaces of the seed pieces when planted act as avenues of attack by staphylinids.

[7] These insect determinations were made by the late Dr. C. R. Phipps, at that time entomologist of the Maine Agricultural Experiment Station.

FIELD OBSERVATIONS ON INSECTS THAT COMMONLY ATTACK POTATO SEED PIECES IN AROOSTOOK COUNTY

When freshly cut seed pieces are exposed in the field, soft rots often develop. From such rotted seed pieces the writer has reared a number of dipterous insects. Among these are the common housefly (*Musca domestica*), the seed-potato maggot (*Hylemyia trichodactyla* Rond.), the seed-corn maggot (*H. cilicrura* Rond.), and two pomace flies (*Drosophila funebris* Fab. and *D. bruschii* Cog.).[8] In such decayed potato material a histerid beetle also has been commonly observed.

In Aroostook County very often planted seed pieces are injured by a wireworm (*Cryptohypnus abbreviatus* Say.). In 1928 and 1929 approximately 25 percent of the seed pieces in one experiment were attacked by this insect. During 1930 the writer examined approximately 2,000 seed pieces of which 40 percent had been injured by wireworms. Although a high proportion of the seed pieces had been injured by the burrowing of these insects, the economic loss appeared to be quite negligible and the seed pieces germinated well. *C. abbreviatus* apparently attacks healthy seed pieces and has never been observed by the writer to be a carrier of bacterial decay, although in a few instances a slight fungus decay has been noted about the tunnels. This species of wireworm attacks healthy seed pieces in contrast with the habits of some other insects common in potato fields which are apparently attracted to decaying organic matter. The writer feels that this particular species of wireworm does not play an important role in the dissemination of blackleg and seed-piece decay.

The writer has examined numerous decayed potato seed pieces in the field. During 1927 and 1928 practically all the decayed seed pieces in fields showing blackleg were infested by the seed-corn maggot or the potato-seed maggot. In these same fields the healthy seed pieces were free from maggot attack. During the season of 1932, approximately 2,000 individual seed pieces were examined; only 2 showed bacterial decay, and each of these contained approximately 40 larvae of the seed-corn maggot. The writer has never noted healthy potato seed pieces infested by either of these insect larvae. The seed-corn maggot is generally present, however, when the seed pieces contain a bacterial decay and are exposed to the conditions of the soil in the field.

Adult and larval stages of the larder beetle (*Dermestes lardarius*) are also very prevalent about decaying seed pieces and plants affected with blackleg.

Staphylinids are often abundant wherever decaying potato tubers are present in the soil. Observations have shown that these insects are probably the most abundant and appear to have some relation to seed-piece decay and blackleg. The larvae and also the adults are very active feeders and are found burrowing into seed pieces and plants affected with blackleg.

SUMMARY

The studies presented in this paper were conducted to determine the part taken by certain insects in the dissemination of blackleg and

[8] These insect determinations were made by the late Dr. C. R. Phipps, at that time entomologist of the Maine Agricultural Experiment Station.

seed-piece decay in the potato, the factors which influence the attack by insects, and the consequent development of these diseases.

The seed-corn maggot (*Hylemyia cilicrura* Rond.), a common insect in Maine, may injure planted potato seed pieces. The life history and the habits of this insect were studied.

The seed-potato maggot (*Hylemyia trichodactyla* Rond.), also attacks potato seed pieces in Maine. The data indicate that this insect has a more specific preference for potato tissue in Maine than does *H. cilicrura*. Its habits and life history are similar to those of *H. cilicrura*.

Soft rot and other pathogenic bacteria are intimately associated with the different stages in the development of the seed-corn maggot both in Maine and South Carolina and were isolated from the surface of eggs and from within the puparia and the adult. Bacteria capable of producing blackleg and decay in potatoes were isolated from puparia of the seed-corn maggot that had over-wintered in potato fields of Aroostook County, Maine.

The soft-rot organism appeared to aid in the development of the seed-corn maggot when present on agar media in which they were feeding. The presence of other soil organisms was, however, much more important in promoting a rapid growth of this insect.

Blackleg and seed-piece decay were produced in Maine under laboratory conditions by inoculations with the seed-corn maggot and the seed-potato maggot. The seed-corn maggot also successfully inoculated potato seed pieces and slices with *Erwinia carotovora* and other pathogenic bacteria under controlled conditions in the laboratory in South Carolina. The adult insect of the seed-corn maggot did not successfully inoculate potato seed pieces with pathogenic bacteria by mere contact under field conditions in South Carolina. These insects were not found in potato bins.

Field and laboratory studies show that these insects will not attack seed pieces that are free from decay. They generally are attracted to bacterial lesions on seed pieces, or to seed pieces that have been injured by fertilizer burning or by desiccation. The maggots were not attracted to lesions which were caused by *Phoma tuberosa* and other fungi and which were free from bacteria.

Shallow surface lesions are formed when unsuberized seed pieces are planted in moist, warm soil in South Carolina. The young contaminated larvae of the seed-corn maggot migrate and enter the seed pieces through these lesions. The insects aggravate the decay by their burrowing, and the seed pieces are completely destroyed if the soil moisture content is relatively high.

Suberizing the cut seed prevents the formation of the primary lesions through which the maggots enter and this eliminates the injury caused by the insects in the South.

In Aroostook County seed pieces do not normally develop surface lesions as a result of soil contamination such as occurs in the South, and the attack by the seed-corn maggot and the seed-potato maggot occurs through lesions on potatoes in the bin prior to their being planted.

Freshly cut potato seed may be safely planted in Aroostook County without danger of injury by maggots.

Freshly cut seed pieces when injured by excessive drying often develop a softened condition on their cut surfaces, and bacterial con-

tamination may become established there. The seed-corn maggot and the seed-potato maggot attack the seed pieces through these diseased areas.

Seed pieces that have been injured by maggots may decay rapidly provided the soil is sufficiently wet.

Certain other insects are commonly associated with decaying potato parts in the field and in the storage bins of Maine but apparently do not have a part in bringing about these conditions. Among these insects are the common housefly (*Musca domestica*), the false cranefly (*Trichocera* sp.), two pomace flies (*Drosophila funebris* Fab. and *D. bruschii* Cog.), the fungus gnat (*Sciara tridentata*), and the larder beetle (*Dermestes lardarius*).

The wireworm larvae (*Cryptohypnus abbreviatus*) often attack potato seed pieces in northern Maine, but their presence has not been associated with a bacterial decay.

A certain staphylinid was found associated with decaying seed pieces and with plants affected with blackleg. This insect may aid in the dissemination and the destruction of potato seed pieces in Maine.

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SUSCEPTIBILITY OF SPECIES OF CUPRESSACEAE TO CROWN GALL AS DETERMINED BY ARTIFICIAL INOCULATION[1]

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INTRODUCTION

The natural occurrence of crown gall on conifers has been reported by Persons (*2*)[2] and by Barrus, Boyd, and Wood[3] on *Juniperus sabina;* by Brown and Evans (*1*) on *Cupressus arizonica;* by Smith (*5*) on *Libocedrus decurrens;* by Metcalf,[4] who observed large galls at and below the ground level on a street tree of *Araucaria bidwillii;* and by Rounds,[5] who found a gall 10 inches in diameter on *Araucaria excelsa.*

Crown gall has been artificially produced on *Sequoia gigantea* and *S. sempervirens* (*3*), on *Araucaria bidwillii* (*4*), *Libocedrus decurrens* (*5*), *Cupressus* spp. (*7*), and on *Taxus baccata* var. *erecta* (*6*).

The results of artificial inoculations on species of Cupressaceae with *Bacterium tumefaciens* Smith and Townsend (*Phytomonas tumefaciens* (Smith and Town.) Bergey et al.) are reported in this paper. The cultures of the organism used in the inoculations were isolated from *Prunus persica, Libocedrus decurrens,* and *Salix* sp.

MATERIALS AND METHODS

The Cupressaceae under investigation consisted of species of *Cupressus, Juniperus, Libocedrus, Thuja, Thujopsis,* and *Chamaecyparis.*

The plants used in this experiment were: (1) Small seedlings obtained from the Rancho Santa Ana Botanic Garden; (2) plants from the United States Department of Agriculture carrying the plant introduction numbers; (3) small trees purchased from a local nursery; (4) rooted cuttings from certain species; (5) plants grown from seed at the University of California Citrus Experiment Station; and (6) large trees growing on the campus. The sources of the plants are shown in table 1. Seedlings and small trees were grown in 5-gallon tin containers in a lath house during the experiment and were in a vigorous growing condition.

Inoculations were through wounds made by a steel needle or through deeper wounds made by cutting through the inoculum into the tissue with a scalpel. The wounds were left unprotected or were protected in various ways. In some tests the wounds were wrapped with paraffin paper. Desiccation in other tests was further checked by tying moist cotton over the wounds, which were then wrapped with paraffin paper fastened at the ends to the plant with nurseryman's

[1] Received for publication June 5, 1939. Paper No. 404, University of California Citrus Experiment Station.

[2] Italic numbers in parentheses refer to Literature Cited, p. 925.

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[4] Letter dated March 5, 1938, to the author from Woodbridge Metcalf, extension forester, University of California.

[5] Oral report to the author July 8, 1939, by M. B. Rounds, Associate in the Citrus Experiment Station.

tape. When inoculations were made near the base of the tree, a waterproof plant pot was placed around the inoculated trunk and filled with fine gravel which was kept moist. A few inoculations were made on the trunk at and below the ground level. Some of the smaller plants were inoculated and kept for a time in a moist chamber, and galls were frequently developed by the use of this method when results from unprotected inoculation wounds had failed. Positive results were obtained from all of these methods on susceptible hosts.

TABLE 1.—*Summary of artificial inoculations through wounds with Bacterium tumefaciens on species of Cupressaceae*

Host species	Sources of plant material [1]	Inoculations	Galls [2]	Gall diameter range [2]
		Number	*Number*	*Millimeters*
Cupressus arizonica Greene	Seedlings	93	18	5–20
Do	S 2357, S 2358	35	7	5–15
Cupressus bakeri Jeps	S 2127, S 2131	30	4	3–30
Cupressus benthami Carr	SPI 114036	15	7	5–20
Cupressus duttoni Jeps	S 2157	15	7	3–25
Cupressus forbesii Jeps	S 2315, S 2319, S 2335	50	9	4–20
Cupressus glabra Sudw	SPI 112084	20	0	0
Do	C. E. S., Nursery	155	0	0
Cupressus guadalupensis Wats	S 2099	35	0	0
Cupressus goveniana Gord	S 2181, S 2182	30	2	3–20
Cupressus lusitanica Mill	SPI 73844	60	5	10–25
Cupressus knightiana Mast	Nursery	10	3	2–3
Cupressus macrocarpa Hartw	S 2177, S 2184	25	7	3–35
Do	Seedlings	165	3	2–20
Cupressus macnabiana Murr	S 2118, S 2154	25	2	2–20
Cupressus montana Wigs	S 2067	30	0	[3]
Cupressus nevadensis Abrams	S 2159	15	3	3–5
Cupressus pygmaea Sarg	S 2133, S 2137	30	7	6–35
Cupressus sargentii Jeps	S 2156, S 2149, S 2185	43	10	12–35
Cupressus sempervirens L	C. E. S	45	9	10–20
Cupressus thurifera Schlecht	S 2356	28	4	5–25
Cupressus torulosa Don	SPI 112085	15	4	3–10
Thuja plicata Don	Nursery	45	9	10–20
Thuja occidentalis L	do	100	5	5–25
Thuja orientalis L	C. E. S	30	17	10–30
Thujopsis dolabrata Sieb. and Zucc	Nursery	45	2	10–15
Chamaecyparis lawsoniana Parl	do	90	2	0
Libocedrus decurrens Torr	do	95	34	10–30
Juniperus ashei Buchholz	SPI 124965	6	3	[3]
Juniperus californica Carr	C. E. S	95	0	0
Juniperus cedrus Webb and Berth	SPI 57080	50	2	[3]
Juniperus hibernica Gord	Nursery	35	4	[3]
Juniperus phoenicea L	SPI 65020	20	6	5–15
Juniperus procera Hochst	SPI 60553	30	3	5–10
Do	SPI 27505	50	0	0
Juniperus virginiana L	Nursery	35	15	5–20

[1] By "seedlings" is meant plants grown from seed at the University of California Citrus Experiment Station. "S" denotes the accession number of plants from the Rancho Santa Ana Botanic Garden, and "SPI", the plant introduction number of plants from the U. S. Department of Agriculture. "C. E. S." indicates large trees growing on the campus of the Citrus Experiment Station, and "Nursery" indicates trees purchased from a local nursery.

[2] Results observed 6 months to 1 year after inoculation.

[3] Knobs.

Control punctures were made on the various hosts inoculated, but because of the limited plant material available, these controls were not numerous.

GALLS ON CUPRESSUS

The results of inoculations on species of *Cupressus* are listed in table 1. Galls (fig. 1) developed on all species tested, with the exception of *guadalupensis*.

The results on *glabra* and *montana*, however, were somewhat inconclusive. On small trees of *glabra* (*C. arizonica* var. *bonita*) the inoculations caused the development of small knoblike projections

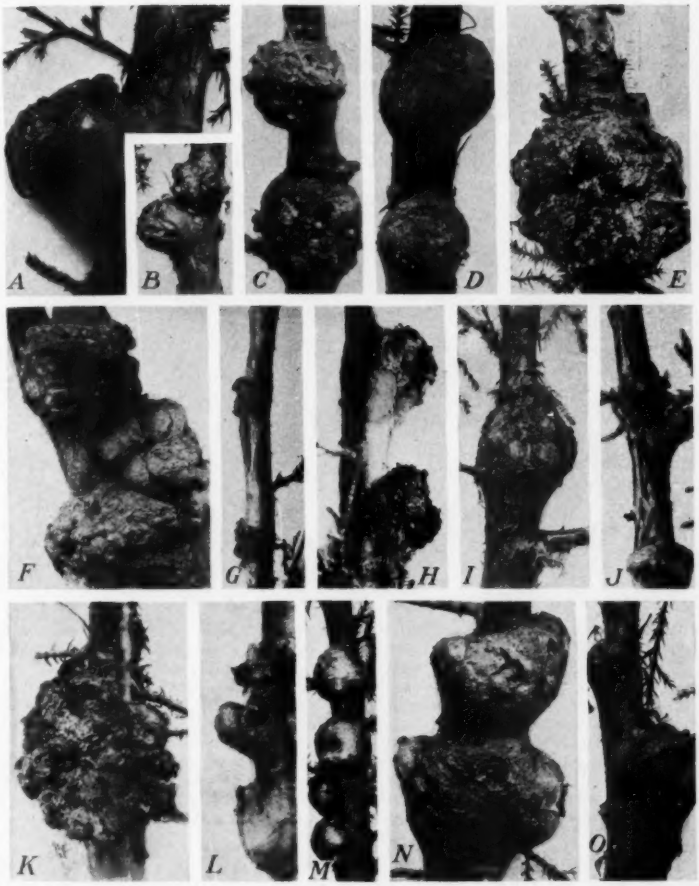

FIGURE 1.—Artificial galls produced on species of *Cupressus* by inoculation with *Bacterium tumefaciens* isolated from *Salix* sp. for all galls except *G* and *H*, for which cultures were isolated from *Prunus persica*. The time, in months, from the date of inoculation to the date of the photograph is indicated in parentheses following the description of the species: *A*, *arizonica*, a seedling (24 months); *B*, *arizonica*, S 2357 (14 months); *C*, *macnabiana*, S 2154 (18 months); *D*, *sargentii*, S 2149 (19 months); *E*, *macrocarpa*, a seedling (26 months); *F*, *benthami*, SPI 114036 (12 months); *G*, *lusitanica*, SPI 73844 (8.5 months); *H*, same galls (24 months); *I*, *thurifera*, S 2356 (8 months); *J*, *torulosa*, SPI 112085 (5.5 months); *K*, *goveniana*, S 2181 (26 months); *L*, *forbesii*, S 2335 (26 months); *M*, *pygmaea*, S 2137 (14 months); *N* *bakeri*, S 2131 (14 months); *O*, *duttoni*, S 2157 (8.5 months).

that failed to become typical galls (fig. 2, *F*). On mature trees of *glabra* growing on the campus, 50 series of 3 to 5 puncture inoculations each, were all negative. (*Guadalupensis* and *glabra* are the species of *Cupressus* frequently grown as ornamentals in southern California.) The galls on *montana*, 4 months after inoculation, were small knoblike growths 1 to 3 mm. in diameter that had grown from healed-over tissue (fig. 2, *D*, *E*). Although later observations indicated that these galls increased somewhat in size, their slow development suggests that the species has strong resistance. A few typical galls formed on *forbesii*, but most of the inoculations were negative in effect.

FIGURE 2.—Artificial galls produced on various species of Cupressaceae. Inoculations of *A*, *D*, *E*, and *F* were by cultures isolated from *Salix* sp.; inoculations of *B* were by cultures from *Prunus persica*, and inoculations of *C* were by cultures from *Libocedrus decurrens*. The time, in months, from the date of inoculation to the date of the photograph is indicated in parentheses following the description of the species: *A*, *Thujopsis dolabrata* (9 months); *B*, *Chamaecyparis lawsoniana* showing two overgrowths with small projections on their upper parts and between these overgrowths a small knoblike development (11 months); *C*, *Libocedrus decurrens* showing two galls, the upper gall smooth and the lower gall rough (24 months); *D*, *E*, *Cupressus montana*, S 2067, small knoblike galls (4 months); *F*, *C. glabra*, knoblike projections (4 months).

The aerial gall on *Cupressus* may first appear as a globose swelling having a smooth bark from which small projecting knobs are often developed. This bark covering may remain smooth for about a year, but often the pressure of growth causes it to crack, and gum forms. The gall eventually becomes rough and resembles crown gall as it forms on other susceptible hosts. The artificial galls that develop below the soil are usually softer than aerial galls and have a smoother bark. The most susceptible species of *Cupressus* are probably *macrocarpa*, *pygmaea*, *thurifera*, *sargentii*, *lusitanica*, *duttoni*, and *arizonica*; but too few inoculations were made to permit definite conclusions to be drawn.

GALLS ON JUNIPERUS

The galls produced from inoculations on species of *Juniperus* are listed in table 1. The number of species available for testing was some-

what limited. Growths resulting from inoculations on *hibernica* were small papillalike protuberances that failed to develop into typical galls but were probably definite responses to the stimulus of the inoculation organism. The results of these inoculations were so inconclusive, however, as best to be regarded as negative. The inoculations on *cedrus*, SPI 57080, at first showed small overgrowths 2 to 3 mm. in diameter (fig. 3, *F*) that were regarded as gall initials; but these gall-like structures soon ceased to increase in size and, later, almost disappeared. Galls were readily formed on *virginiana* and *procera*, SPI 60553. Results on another tree of *procera*, SPI 27505,

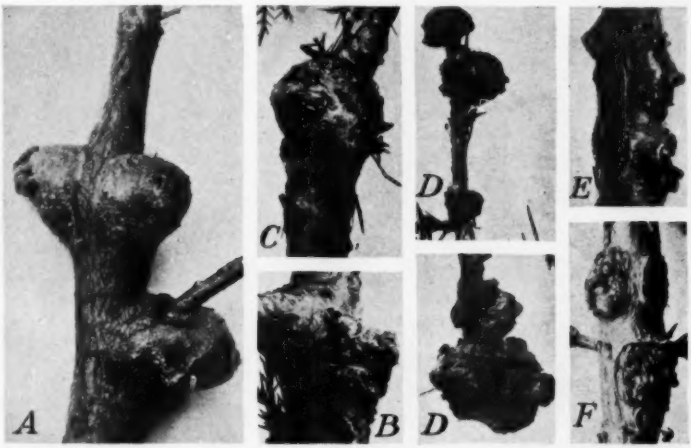

FIGURE 3.—Artificial galls produced on species of *Juniperus*. Inoculations of *A*, *B*, and *D* were by crown gall cultures from *Salix* sp.; inoculations of *C*, *E*, and *F* were by cultures isolated from *Prunus persica*. The time, in months, from the date of inoculation to the date of the photograph is indicated in parentheses following the description of the species: *A*, *procera*, SPI 60553 (14.5 months); *B*, *procera*, SPI 60553 (9 months); *C*, *virginiana*, nursery (15 months); *D*, *virginiana*, nursery (10 months); *E*, *hibernica*, nursery (18 months); *F*, *cedrus*, SPI 57080 (12 months).

were negative after 50 inoculations. Negative, also, were inoculations on *californica*. From the results of these inoculations it appears that *Juniperus* spp. are less susceptible than *Cupressus* spp. to inoculation with *Bacterium* (*Phytomonas*) *tumefaciens*.

GALLS ON LIBOCEDRUS

Nursery seedlings of *Libocedrus decurrens* were tested, and this host proved extremely susceptible to artificial inoculation. Galls frequently developed with a smooth bark, as shown in the upper gall of figure 2, *C;* but after about a year these smooth galls usually ruptured from growth pressure and became like galls on other susceptible hosts. The formation of galls on *L. decurrens* from artificial inoculations in earlier tests has already been described (5).

GALLS ON THUJA AND THUJOPSIS

Galls produced by inoculations on species of *Thuja* are listed in table 1 and shown in figure 4. The three species, *plicata*, *occidentalis*, and *orientalis*, responded readily to artificial inoculation and were apparently among the most susceptible species of the Cupressaceae. The galls were rough almost from the first.

Thujopsis dolabrata was more difficult to infect than were the species of *Thuja*. Forty inoculations on a plant 2 feet high gave negative results. Rooted cuttings from this plant, however, proved susceptible and developed typical rough galls (fig. 2, *A*).

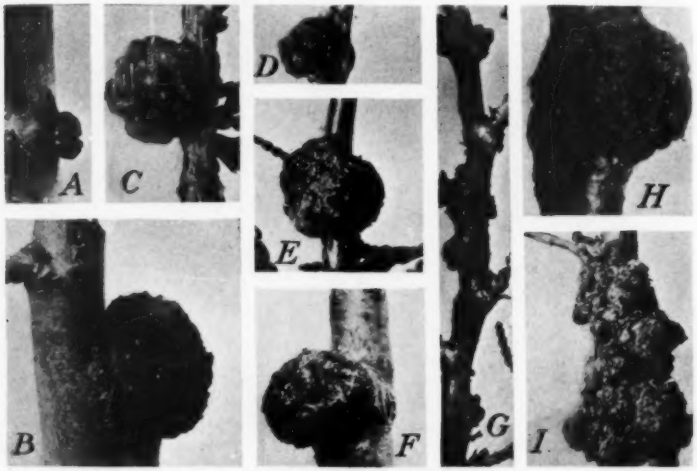

FIGURE 4.—Artificial galls produced on nursery trees of species of *Thuja*. Inoculations of *A* to *H* were by cultures isolated from *Prunus persica;* inoculations of *I* were by cultures from *Salix* sp. The time, in months, from the date of inoculation to the date of the photograph is indicated in parentheses following the description of the species: *A*, *Thuja plicata* (14 months); *B*, same gall (17 months); *C*, *plicata* (14 months); *D*, *occidentalis* (16 months); *E*, *occidentalis* (15 months); *F*, same gall (19 months); *G*, *orientalis* (10 months); *H*, *orientalis* (24 months); *I*, *orientalis* (24 months).

GALLS ON CHAMAECYPARIS

The Lawson cypress (*Chamaecyparis lawsoniana*) was the only species of *Chamaecyparis* tested. Ninety inoculations were made on three host trees, and the results of all except three were negative. Of these three inoculations, which were inconclusive, two showed overgrowths having smooth surfaces with small projections on their upper parts (fig. 2, *B*). At the time of the writing of this report, 4 years after inoculation, no abnormal increase in the size of these overgrowths has taken place, and they are less gall-like in appearance. Between the upper and lower overgrowths (fig. 2, *B*) can be seen a knoblike development which may have increased slightly in size; it is now 5 mm. in diameter and extends 6 mm. from the branch. The susceptibility of this species to artificial inoculation with the crown gall organism is yet to be demonstrated.

SUMMARY

This paper reports the results of artificial inoculations made with *Bacterium tumefaciens* Smith and Townsend on species of Cupressaceae. Cultures isolated from *Prunus persica* produced galls on *Cupressus*, *Juniperus*, and *Thuja*. Cultures from *Salix* sp. produced galls on *Cupressus*, *Thujopsis*, *Juniperus*, and *Thuja*. Cultures from *Libocedrus decurrens* gave negative results on all species except *L. decurrens*.

Sixteen species of *Cupressus* proved susceptible to inoculation. On *glabra* and *montana* occasional knoblike growths were formed, but no typical galls developed. One species of *Cupressus* (*guadalupensis*) was apparently resistant, as the results of all inoculations were negative. Inoculations on species of *Juniperus* produced galls on *virginiana* on *phoenica* and on one plant of *procera*, but only small knoblike growths on *hibernica*, and *cedrus*. *Libocedrus decurrens* and the three species of *Thuja* tested proved susceptible and responded readily to inoculation. The original plant of *Thujopsis dolabrata* was negative in response, but rooted cuttings from this plant developed typical rough galls. *Chamaecyparis lawsoniana* developed nontypical overgrowths.

Control punctures were made on the various hosts inoculated. All of these injuries healed over in a normal manner.

The results of inoculations on species of Cupressaceae suggest the relative resistance of the various species but are not conclusive because of the differences in the environmental conditions of the plants tested and the small number of inoculations on some of the species.

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